
A REVISION OF THE FERN GENUS *PHANEROPHLEBIA* (DRYOPTERIDACEAE)¹

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ABSTRACT

The primarily neotropical fern genus *Phanerophlebia* is revised taxonomically to include eight species, with a key and descriptions provided. Classification of the genus within the Dryopteridaceae is reviewed, as are the morphology, stelar anatomy, and cytology of the species. The justification for reduction of *Phanerophlebia remotispora* to a variety of *P. nobilis* is discussed. The recently named diploid species, *P. gastonyi*, is contrasted with its tetraploid derivative, *P. juglandifolia*, and hybridization and polyploidy within the genus are summarized.

Phanerophlebia C. Presl is an enigmatic genus comprising eight species of terrestrial ferns of the New World tropics and adjacent subtropical regions. Most pteridologists know little about the group because of the rarity with which the species are encountered in nature. The genus was revised taxonomically by Underwood (1899) and Maxon (1912). Both of these early studies were based on relatively few herbarium specimens and did not adequately circumscribe variation in critical morphological characters, resulting in many subsequent misdeterminations.

The need for a new taxonomic study of this genus was further supported by disagreements and questions raised by the few researchers who have examined the species in recent years. Smith (1981), Mickel and Beitel (1988), and Stolze (1981), in their detailed floristic treatments of pteridophytes of Chiapas and Oaxaca, Mexico, and Guatemala, respectively, each pointed out taxonomic problems in the group and emphasized different characters in delineating taxa. Tryon and Tryon (1982), in their review of American ferns, pointed out the confusing pattern of morphological variation in the genus and suggested that some of the traditionally accepted species might be combined, following much-needed, critical, future studies.

Aside from questions of species-level taxonomy, *Phanerophlebia* has also provided problems in generic classification. The distinctness of the group from Asiatic *Cyrtomium* and nearly cosmopolitan *Polystichum* has remained controversial and is symptomatic of the general difficulties of generic circumscription present in the family Dryopteridaceae (and in several other pteridophyte families as well).

The present paper incorporates data from several concurrent studies (Stein et al., 1989; Yatskievych, 1989, 1990, 1992, 1993; Yatskievych & Gastony, 1987; Yatskievych et al., 1988) on aspects of evolution and systematics of *Phanerophlebia* and the results from field, herbarium, and greenhouse studies on the group, in an attempt to refine our understanding of the genus. An evolutionary species concept is employed, which circumscribes a set of morphologically defined taxa that are also genetically separated. Genetic separation, based on various estimates of genetic similarity, rather than crossing barriers, has been used, because attempts at artificial hybridization between taxa failed uniformly (unpublished data). The varietal designation is used in this paper to denote putatively interfertile morphotypes within a species, which lack sharp biogeographic discontinuities, and which are sep-

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arated by only a single, relatively trivial, morphological character (whose genetic basis remains unknown).

METHODS AND MATERIALS

Herbarium specimens, including types, were studied from the following collections: A, ARIZ, ASC, BH, CAS, CM, CR, CU, DS, ENCB, F, GH, HAL, IND, K, LL, MEXU, MICH, MO, NY, P, POM, RSA, TEX, UAMIZ, UC, US, XAL (abbreviations follow those used in Holmgren et al., 1990). Approximately 1400 specimens representing about 670 different collections of *Phanerophlebia* were examined. Additionally, about 260 collections of *Cyrtomium* and *Polystichum* were examined for comparative purposes.

Information from herbarium specimens was supplemented with observations of populations in nature. A total of 25 populations of *Phanerophlebia* was located during fieldwork in the southwestern United States, Mexico, and Costa Rica. In addition to field observations and carefully pressed specimens, representative plants from each population were transplanted into common culture in the Department of Biology greenhouses at Indiana University for further observation of phenotypic variation.

For detailed observations of scale morphology, small strips of clear tape (Scotch) were used to remove samples from leaves and rhizomes with the aid of forceps and mounted on microscope slides in Hoyer's medium. Stelar observations were based on direct observation of freehand sections from living rhizomes. Details of venation patterns and epidermal morphology were observed from pinnae or pinna pieces cleared using the bleaching procedures summarized by Dilcher (1974). Following dehydration and staining with safranin O, samples for observation of leaf venation were dried flat in a small press similar to that described by Wagner (1976), and epidermal samples were mounted on microscope slides in Permount, prior to viewing.

Chromosome counts were made on representatives of each population. Young pinnae with developing sporangia were fixed in Farmer's solution (3:1 absolute ethanol:glacial acetic acid) for meiotic counts. Sporangia were spread using the standard acetocarmine squash technique (Manton, 1950), as modified by Haufler et al. (1985). Cells were examined with a compound microscope and chromosomes were drawn using a camera lucida. New counts or those differing from the literature were also photographed, using Kodak Technical Pan film.

For spore counts, single, unopened sporangia were carefully removed from field-collected (rather than greenhouse-grown), dried pinnae with a dissecting probe and opened in a drop of lactic acid under the dissecting microscope. Ten counts from different sori were compiled for representative plants from each population. Spore sizes were also measured from material in lactic acid, using a compound microscope equipped with an ocular micrometer. Thirty measurements of the longest dimensions of spores from at least five sporangia were made, from which the mean and standard deviation were calculated for each sample. Spore morphology was observed under the compound microscope from material in lactic acid and from dried material, as well as by scanning electron microscopy (SEM). The latter observations were carried out using a Cambridge Stereoscan 250-MK2 machine. Dry spores were mounted on aluminum SEM stubs using double-sided tape without pretreatment and sputter-coated with gold/palladium using a Polaron E5100 unit prior to viewing.

MORPHOLOGY AND ANATOMY

RHIZOMES AND LEAVES

Rhizomes of *Phanerophlebia* species are dictyostelic and anatomically similar to those of *Cyrtomium* species studied by Chandra and Nayar (1982) and Gibson et al. (1984). They range from 3 mm in diameter in small plants of *P. pumila* to ca. 20 mm in *P. macrosora*, but are 8–15 mm in adult plants of most species. Rhizomes may be characterized as generally short-repent (erect or ascending in *P. macrosora* and *P. pumila*), unbranched (tending to branch at maturity in *P. auriculata* and *P. umbonata*), and deep-seated in the substrate (except in *P. gastonyi*, *P. pumila*, and sometimes in *P. juglandifolia*). In all species, the rhizomes are densely covered with scales near the apices and with persistent petiolar bases and adventitious roots on older portions. The dense mat of petioles and roots makes the rhizomes appear larger than they actually are. Rhizome scales are discussed below, under indument.

Leaves (fronds) develop equally from all sides of the rhizomes and are clustered near the rhizome apices. Mature leaves range in length from 4 cm in *P. pumila* to 270 cm in *P. macrosora*. They persist for two or more years and eventually die back to the petiolar bases, which are persistent. There is no well-defined zone of abscission along the petioles. The petiolar bases persist for several years, turning hard and "woody" in *P. macrosora*, but remaining green and semisucculent, with green in-

ternal tissues, in other species. Although an iodine test was not performed, these persistent petiolar bases presumably function as trophopods (Wagner & Johnson, 1983).

Petiole vascularization is simpler than in many other members of the Dryopteridaceae, and the 4–8 vascular bundles (mean = 6) are arranged in an uneven ring. The petioles are curved abruptly at their bases, so as to orient the leaves vertically, except in *P. macrosora*. In this species the petiolar bases are usually oriented horizontally for a distance of 5–10 cm, before curving upward, the leaf bases thus appearing geniculate. Petioles may be shorter than or somewhat longer than the laminae, and are scaly (see below) in all species.

Laminae are monomorphic and 1-pinnate (sometimes simple in *P. gastonyi* and *P. pumila*), with alternate pinnae (leaflets). Rachises are adaxially sulcate, with the groove more or less confluent with the costal groove of each pinna, although, in practice, this character is usually difficult to assess. The laminae have discrete terminal pinnae, but are not typically imparipinnate in that some leaves of all species have an even total number of pinnae. Such leaves are usually mixed on the same plant with those having odd numbers of pinnae, and there is no morphological evidence for the existence of "pseudoterminal" pinnae; i.e., no nodes or articulations are present at the tip of a rachis to suggest suppression of the laminar apex and its replacement by an adjacent, lateral pinna.

Pinnae of all species are chartaceous to subcoriaceous and have shallow, adaxial, costal grooves. They range in shape from ovate to linear-lanceolate and commonly have attenuate apices and asymmetrical bases. Pinna bases are normally more developed acroscopically (Fig. 1), and acroscopic, basal auricles occur commonly in *Phanerophlebia auriculata*, sporadically in *P. pumila*, and rarely in *P. nobilis* (var. *nobilis*). Pinna margins are spinulose-serrulate, the teeth connected by a narrow, white, marginal band of hard tissue, but the density and distribution of the teeth vary. In *P. gastonyi*, the serrulations are confined to the distal half of each pinna, and in *P. juglandifolia* the density of serrulations in proximal portions of the pinnae can vary greatly on individual leaves. In *P. macrosora*, serrulations tend to be somewhat more widely spaced than in other species and the teeth are often somewhat stouter.

Rare individuals of most species (particularly *Phanerophlebia auriculata* and *P. pumila*) have some leaves with the pinnae deeply incised to lacerate, particularly on the acroscopic side (Fig. 1b). The same phenomenon was described by Wagner

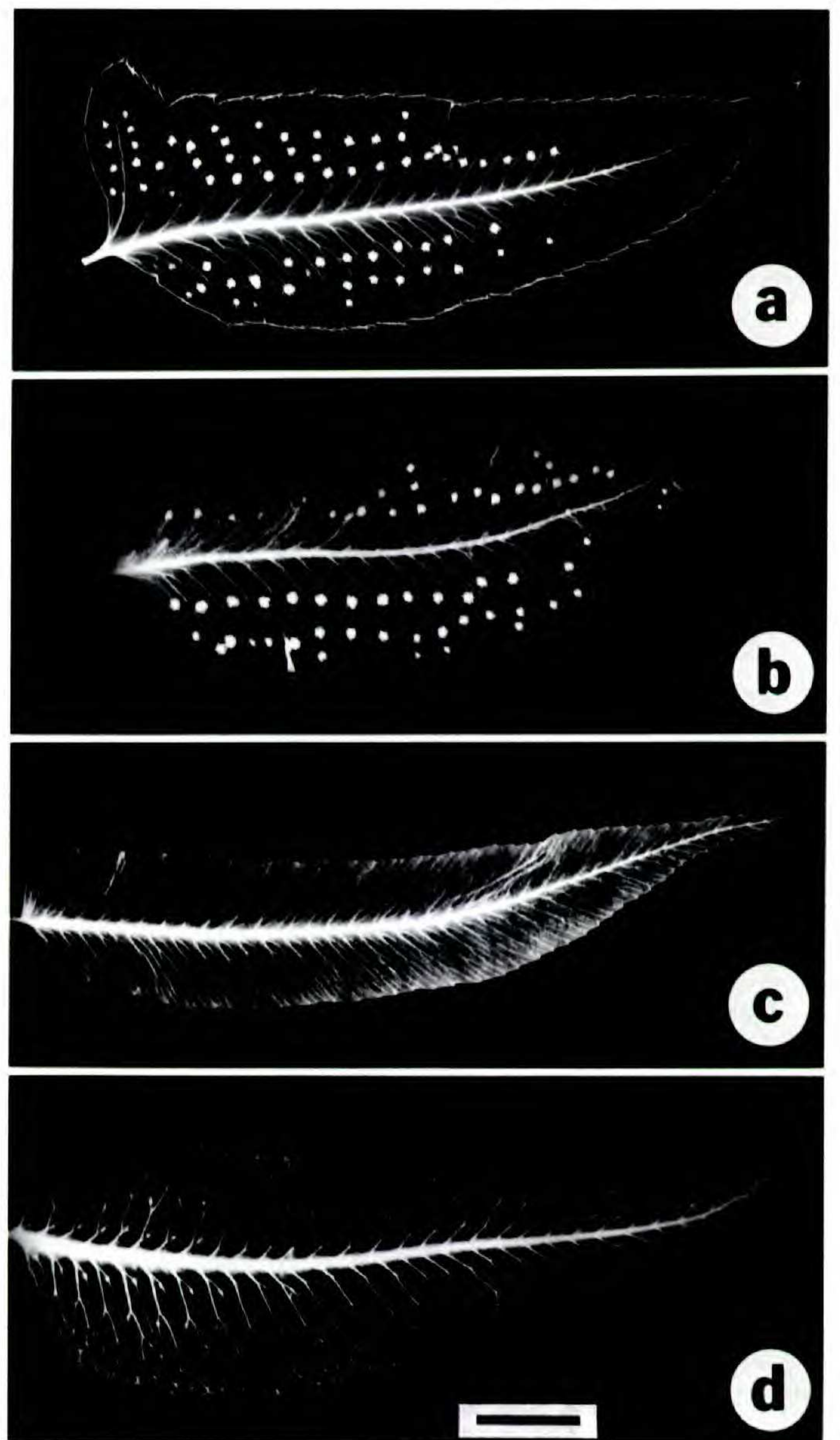


Figure 1. Cleared pinnae of *Phanerophlebia* species. —a. *P. auriculata* (Yatskievych et al. 83–10), showing simple, dichotomous venation and presence of acroscopic, basal auricle. —b. *P. auriculata* (Yatskievych et al. 84–68), showing irregular acroscopic lobing. —c. *P. umbonata* (Yatskievych & McCrary 85–05), showing simple (non-anastomosing), dichotomous venation. —d. *P. gastonyi* (Yatskievych et al. 85–182), showing anastomosing venation. Scale bar = 1 cm.

(1979) for *Polystichum munitum*, and a similar phenomenon in *Polystichum acrostichoides* (f. *incisum* (A. Gray) Gilbert) was attributed by Wagner et al. (1970) to environmental and temporal factors. In *Phanerophlebia*, it is of interest to note that in such pinnae the lobes each contain one vein that has branched from the costa and that the multiserial (with respect to the costa) sori are arranged in a single series on either side of this midvein in each lobe. Such anomalous pinnae provide indirect evidence that the 1-pinnate leaf dissection in *Phanerophlebia* is derived from a more highly dissected leaf type.

Venation in *Phanerophlebia* species is anadro-

mous (this often difficult to observe) and consists of numerous, arcuate, secondary veins branching sequentially from the costa of each pinna (Fig. 1). These secondaries branch 1–4 times before terminating near the pinna margin. There is no vein running parallel to the margins, but there is a thickened, narrow band of hard, white tissue along the edge, at which the veins terminate. Thus, the veins do not extend into the marginal serrulations of the pinnae. The basal 1–2 vein branches do not extend to the margins, instead terminating between the costa and margin. Vein endings are tapered (except those terminating in sori), lacking bulbous thickenings.

The venation pattern of *Phanerophlebia* is of two kinds. The most common type, which characterizes all taxa except *P. gastonyi*, *P. juglandifolia*, and *P. nobilis* var. *remotispora*, consists of simple, dichotomously branched secondaries essentially lacking anastomoses (Fig. 1a–c). All of the free-veined taxa can produce rare, marginal anastomoses, and in *P. haitiensis* these can be fairly common (>2 per pinna, but very irregularly distributed). The ultimate vein-branches in the free-veined taxa range from arcuate to nearly straight, but are usually more or less parallel to one another.

In *Phanerophlebia gastonyi*, *P. juglandifolia*, and *P. nobilis* var. *remotispora*, the branching secondary veins form a regular pattern of 1–3 series of simple, submarginal anastomoses (Fig. 1d). The pattern of reticulation is that of elongate areolae with acute apices and bases. There are no free, tertiary veins included in the reticulations (as in *Cyrtomium*), but in most cases the basal branches of the secondaries end below the anastomoses of adjacent, more marginal branches, thus appearing enclosed. Although there are no clear morphological distinctions between the patterns of reticulation found in the closely related *P. gastonyi* and *P. juglandifolia* on the one hand and those of *P. nobilis* var. *remotispora* on the other, evidence from restriction site polymorphisms in the chloroplast genomes (Yatskievych et al., 1988) and the fact that only one of the two varieties of *P. nobilis* exhibits reticulate venation suggest that this pattern has arisen independently twice in the genus.

Sori of *Phanerophlebia* species are either terminal or lateral on the secondary veins and are situated in 2–4 series (sometimes only 1-seriate in *P. pumila*) between the costa and margin. In *P. umbonata*, the sori are sometimes clustered submarginally, but otherwise they occur in a broad band between the costa and each margin. In *P. gastonyi* and *P. juglandifolia* (occasionally also in other species) the innermost series of sori may be situated

less than 2 mm from the costa, but the innermost sori are otherwise normally more than 4 mm from the costa. This character has been used by some authors to differentiate *P. juglandifolia* from *P. nobilis* var. *remotispora*, but is too variable for consistent application.

The sori are more or less circular and in all but two taxa are covered by an indusium. Presl (1836) first noted the absence of an indusium in *Phanerophlebia juglandifolia* (which he used as evidence to align this species with *Polypodium* under the generic name *Amblia*), but nearly all subsequent workers ignored or dismissed this character until it was reexamined by Smith (1981). *Phanerophlebia gastonyi*, which has been confused with *P. juglandifolia* in the past, is the other species lacking indusia. Part of the problem with regard to this character is that in all of the indusiate species except *P. umbonata* the indusia are fugacious, shriveling and mostly falling off by the time the sorus is mature. Thorough examination of sori in these taxa will always result in the discovery of at least a few remaining, shriveled indusia, however.

In those species possessing indusia, these ephemeral structures are light tan, peltate, roughly circular in outline, erose-margined, and 0.6–1.1 mm in diameter. They are membranous to papery, concolorous, and flat to slightly concave centrally, except in *Phanerophlebia umbonata*, which has firmer, subcoriaceous, persistent indusia with a raised, darkened umbo in the center. Indusia of *P. pumila* are unusual in that the attachment point of the receptacle is sometimes acentric, and the indusia are often more ovate than circular in outline. It is also of interest that although diploid *P. gastonyi* and its tetraploid derivative, *P. juglandifolia*, lack indusia, the rare, sterile, triploid hybrid between the latter taxon and the indusiate *P. macrosora* has rudimentary, irregular indusia less than 0.2 mm in diameter.

SPORES

Spores of selected *Phanerophlebia* species were examined cursorily (usually in conjunction with those of *Cyrtomium*) by several earlier authors, but the first detailed study of spore morphology in the genus appeared as part of the generic treatment for *Cyrtomium* (including *Phanerophlebia*) in Tryon and Tryon's (1982) broad survey of fern genera. The subsequent discussion in Tryon and Lugardon's (1991) survey of fern spores expanded slightly on this initial treatment. The present account attempts to expand upon this excellent foundation.

Sporangia contain 64 spores in all fertile taxa

and are monolet and dark brown at maturity. Spores fall into three size classes. Those of the diploid *Phanerophlebia gastonyi* are 30–42 μm in longest dimension, whereas those of other fertile diploid and tetraploid taxa in the genus are 41–60 μm . Spores of *P. haitiensis*, although seemingly well formed, show great size variation, even within individual sporangia, and measure 36–52 μm . Spore size is thus of little use in identifying polyploids, except as a means of distinguishing *P. gastonyi* from its closest relatives.

The exospore in all species is smooth (Fig. 2) and is covered by a two-layered perispore. The thin, inner perispore has a slightly undulate surface, often also with widely scattered papillae. These papillae may represent the rudiments of columellae that once connected the inner and outer perispore layers, but actual columellae apparently no longer exist. The outer layer of perispore is much thicker than the inner layer and consists of inflated, irregularly undulate folds. The density and degree of inflation of these folds varies developmentally and within each species. They are thus of little use in distinguishing among them, although the mature spores of *P. macrosora* generally have fewer folds than those of other taxa. The surface of the outer perispore layer also varies from nearly smooth to rugulose and contains no observable microperforations.

All fertile specimens of *Phanerophlebia* species possess at least some sporangia that, at maturity, contain malformed, apparently abortive spores of variable size with the outer perispore layer relatively smooth and the folds winglike and uninflated (Fig. 2d). These resemble immature spores in their incomplete perispore deposition and although not obviously collapsed or shrunken within, they will not germinate on agar or soil. Sporangia containing such spores are especially frequent in the relatively few herbarium specimens available of *P. haitiensis*. Whether this phenomenon has a genetic basis is not presently known, but plants placed under environmental stress (such as excess sunlight or high temperature) in the greenhouse produce such abortive spores with greater frequency than when grown under more optimal conditions.

INDUMENT

Leaves of *Phanerophlebia* species do not possess true hairs in the sense that this term is usually applied to such epidermal outgrowths in most ferns. Instead, the uniseriate, multicellular trichomes present in all species are in reality reduced scales, and intergrade completely with the larger, pluriseri-

ate structures usually associated with this term (Fig. 3). Such reduced scales are common in the Dryopteridaceae and have been noted by several students of the family. Daigobo (1972) believed that variations in the pattern of cellular orientation and shape made such trichomes the most stable and important characters for infrageneric classification of the 47 species of *Polystichum* in Japan, Ryukyu, and Taiwan, and applied the name “microscale” to them. Viane (1986), who held trichome morphology to be important in classification of *Dryopteris* species, adopted the name “paleaster” for such hair/scale intermediates. Moran (1986, 1987), working with the related genera *Olfersia* and *Polybotrya*, coined the term “proscale” for them. Smith (1986), in his monograph of *Cyclodium*, differentiated reduced scales from acicular hairs and septate glands also found in that genus but declined to invent a name for these structures. Barrington (1989), in his studies of neotropical *Polystichum*, adopted the term “microscale” and noted that most species of neotropical *Polystichum* shared Daigobo’s (1972) *Metapolystichum* type of scale development.

The pattern of scale development in all species of *Phanerophlebia* is identical and is similar to that seen in the *Metapolystichum* type of Daigobo (1972). The reduced scales found to some degree on the abaxial laminar and distal costular surfaces are tan to brownish and appressed. The smallest are uniseriate and approximately 3 cells long, with somewhat flattened cells and thickened endwalls. In contrast to the situation described by Daigobo (1972) for *Metapolystichum*, however, the terminal cells of these smallest scales are obtuse, rather than acutely attenuate (Fig. 3). Larger scales with two or more cellular series display the morphology more typical of *Metapolystichum* scales. In these larger, reduced scales the basal 1–2 series of cells are smaller than the other cells and are nearly square to rhomboidal in outline. Above this base, the body of the scale is broadened and the individual cells are elongate longitudinally. Processes homologous to the lateral cilia of fully developed costal and petiolar scales are first evident near the base of the reduced scales, which are otherwise entire along their lateral margins.

Along the costae, the reduced scales grade abruptly into the longer and broader structures usually associated with the term scale. Reduced scales are best observed on immature leaves and are apparently shed during development or at least easily abraded from mature laminae. The pinnae of some populations of *P. auriculata* and *P. pumila* possess the densest covering of reduced scales, but this retention of vestiture may be due primarily to the

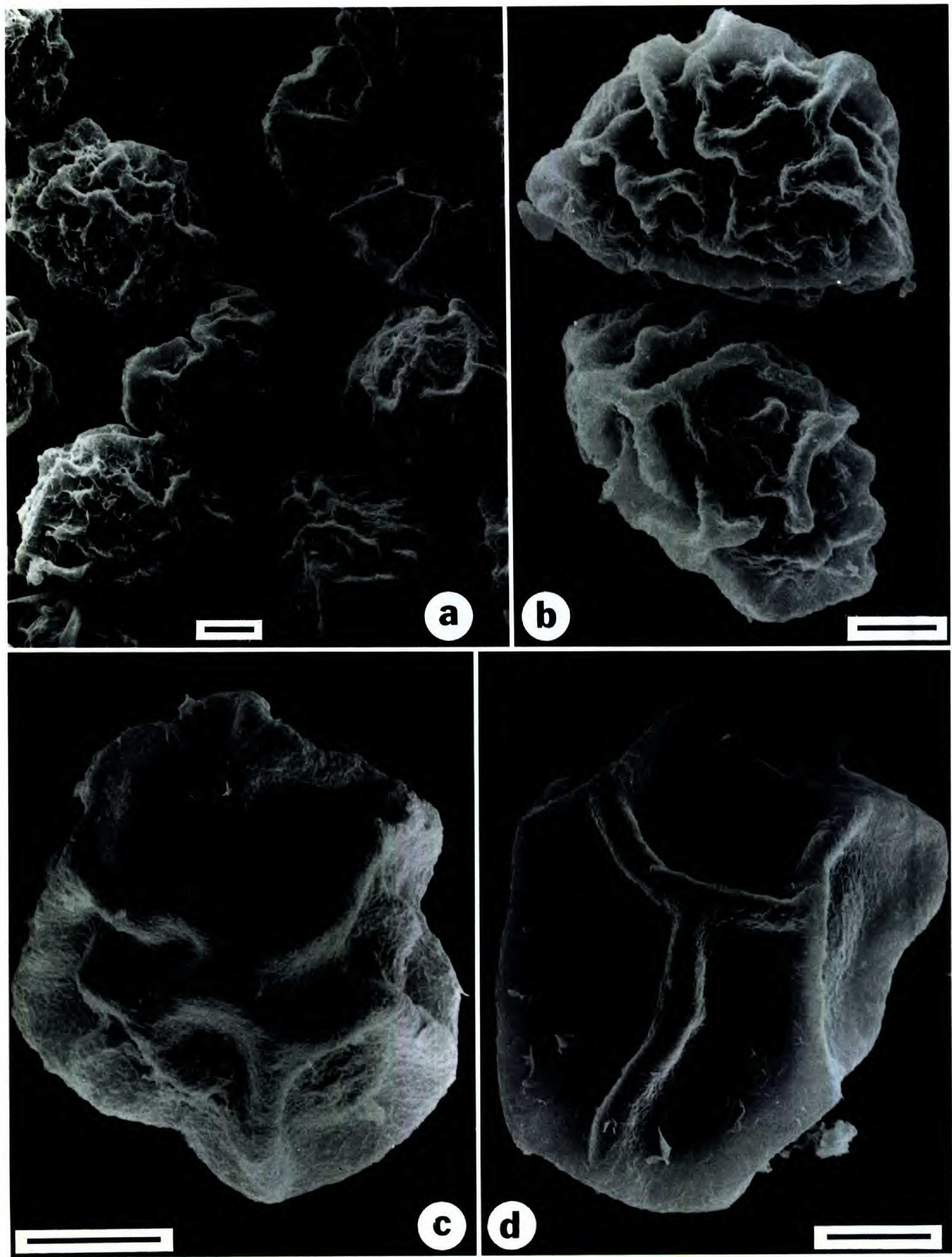


Figure 2. Spores of *Phanerophlebia* species. —a. *P. umbonata* (Yatskievych & Wollenweber 83–87), a mixture of mature and immature spores. —b. *P. auriculata* (Yatskievych et al. 83–10). —c. *P. gastonyi* (Yatskievych et al. 85–182). —d. *P. macrosora* (Yatskievych & McCrary 86–30), with incomplete perispore formation characteristic of nonfunctional spores present in some sporangia of all species. Scale bars = 10 µm.

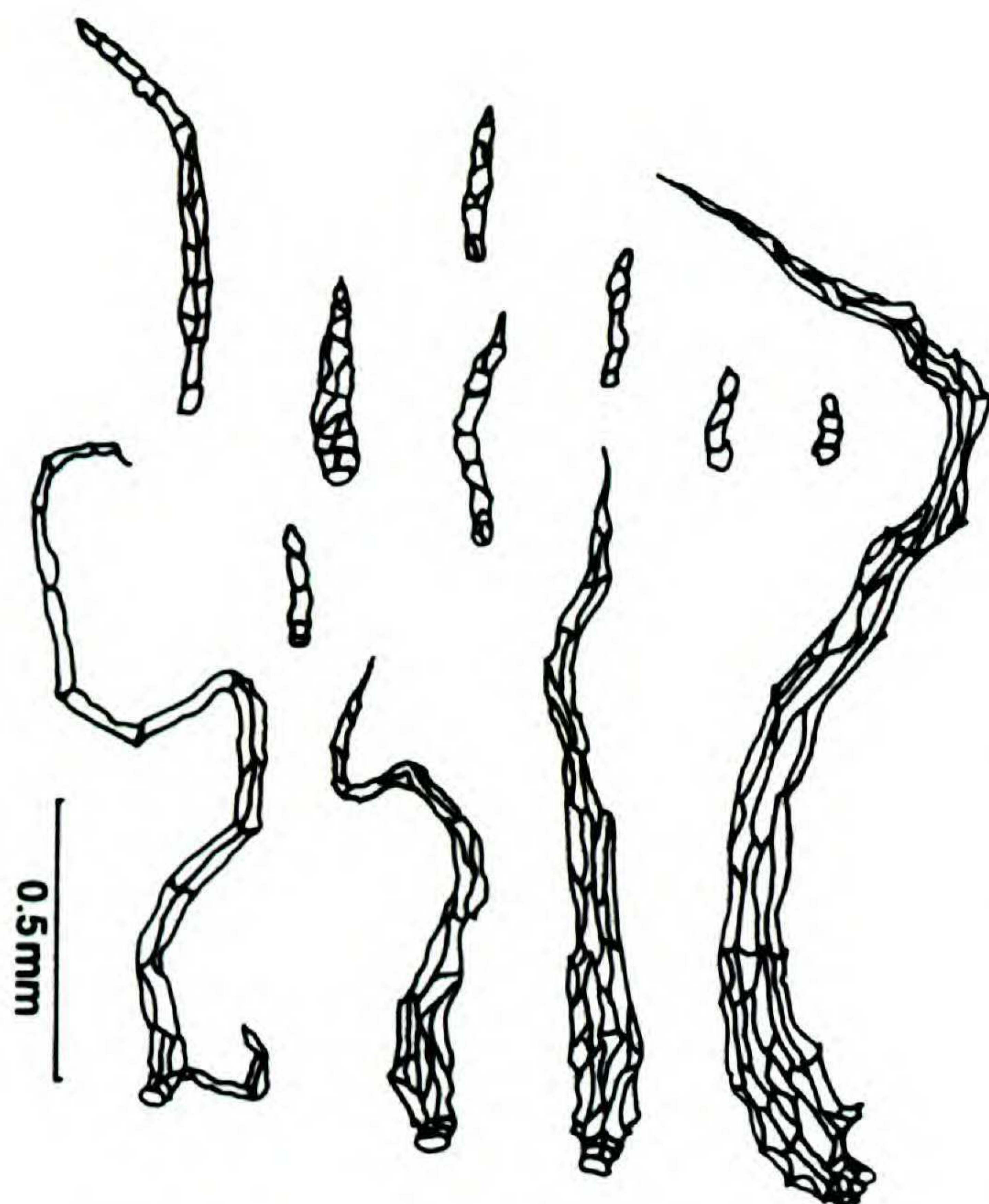


Figure 3. Representative laminar scales from a single leaf of *Phanerophlebia auriculata* (Yatskievych et al. 83–10).

protected habitats in which these plants usually grow.

The most highly developed scales occur along the proximal portions of the petioles and on the rhizomes. The rhizome and largest petiolar scales are similar in morphology within most species, but the rhizome scales are usually less variable and often slightly smaller and more densely ciliate along their margins than those of adjacent petiole bases. The largest rhizome and petiolar scales range in length from 2.5–4.0 mm in *P. gastonyi* to 10–15 mm in *P. macrosora*. Rhizome scales are ovate to elliptic-lanceolate, but petiolar scales vary from linear to ovate in most species, due to the gradation of mixed scale types described above. Exceptions are *P. gastonyi*, which has very few narrower scales mixed with the sparse, ovate scales along the petiolar bases, and *P. pumila*, which has only linear-filiform petiolar scales except in the very basal portions.

The margins of the rhizome and petiolar scales are ciliate, and those of *Phanerophlebia macrosora* are strongly erose-ciliate. In all taxa, there is a tendency for these cilia to break off with age. In *P. nobilis*, cilia tend to be abraded easily, and a diligent search with a dissecting microscope is necessary to observe the few remaining on scales at rhizome or leaf maturity. In contrast, the margins of petiolar scales in *P. gastonyi*, *P. juglandifolia*,

and *P. macrosora* tend to remain relatively unaltered at maturity, although the cilia become abraded with age. The petiole bases of young leaves in all species are covered with a dense indument of imbricate scales except in *P. gastonyi*, wherein the scales are sparser and essentially non-overlapping. In *P. macrosora*, the dense, chaffy covering of scales is especially persistent, even with age.

Rhizome and petiolar scales are concolorous, except in *Phanerophlebia gastonyi* and *P. juglandifolia*. The former species has scales with broad, dark centers of sclerified cells and narrow, hyaline margins. In the latter species the darker, central band is of variable width, though well defined from the correspondingly broader, hyaline margins. Specimens of *P. macrosora* rarely have scales with slightly darker, poorly differentiated, central regions. Otherwise scales of this species are light tan. The remaining taxa produce tan to orange-brown scales; those of *P. nobilis* and *P. umbonata* are usually a pronounced orange-brown in color.

HYBRIDIZATION AND POLYPLOIDY

Chromosome counts for *Phanerophlebia* species are presented in Table 1. These indicate that the base number for the genus is $x = 41$, a common number in the Dryopteridaceae. Representative chromosome counts had been published previously for most species and appeared to indicate a relatively simple cytological situation in the group, with less polyploidy and hybridization than is typical in *Polystichum* and other related genera. The earliest reports for the genus were diploid counts for *P. umbonata* (Wagner, 1963; Mickel et al., 1966). Diploid counts had also been published for *P. juglandifolia*, *P. macrosora*, *P. nobilis*, and *P. remotispora* (Smith & Mickel, 1977). Two tetraploid taxa had been identified, *P. auriculata* (Reeves, 1978) and *P. pumila* (Smith & Mickel, 1977), and except for a single tetraploid count for a sample tentatively ascribed to the otherwise diploid *P. nobilis* var. *remotispora* (Smith & Mickel, 1977, reported as *P. cf. remotispora*), there was no evidence of cytological heterogeneity in any of the species. The only presently accepted species for which no chromosome count exists is *P. haitiensis*, which is known historically from very few collections and is presumed extinct at its type locality in Haiti.

New counts reported in Table 1 agree with most earlier counts for the genus, but document the surprising find that *Phanerophlebia juglandifolia*, as traditionally circumscribed, comprises two cytotypes (Yatskievych & Gastony, 1987). The previously published count from Oaxaca, Mexico (Smith

Table 1. Chromosome numbers in *Phanerophlebia*. All counts are from meiotic material. Vouchers for new counts are accessioned at IND and MO, with duplicates to be distributed elsewhere.

Species	Number of Meiotic Bivalents	Source
<i>P. auriculata</i>	82	U.S.A. Arizona : Chochise Co., Bass Canyon, Galiuro Mtn., 3 Jan. 1983, <i>Yatskievych et al.</i> 83-10; Garden Canyon, Huachuca Mtn., 17 May 1983, <i>Yatskievych</i> 83-161; Santa Cruz Co., Sycamore Canyon, Pajarito Mtn., 30 Dec. 1982, <i>Yatskievych & Yatskievych</i> 82-273; Yavapai Co. (Reeves, 1978). New Mexico : Dona Ana Co., Ice Canyon, Organ Mtn., 21 July 1984, <i>Yatskievych et al.</i> 84-68.
<i>P. gastonyi</i>	41	MEXICO. Chiapas : ca. 13 km N of Berriozabal, 17 July 1985, <i>Yatskievych et al.</i> 85-182. Oaxaca : (Smith & Mickel, 1977, as <i>P. juglandifolia</i>). Veracruz : 1 km N of Pas de Enriquez on rd. from Jalapa to Misantla, 29 Sep. 1986, <i>Yatskievych & Gastony</i> 86-337.
<i>P. juglandifolia</i>	82	MEXICO. Chiapas : (Smith & Mickel, 1977, as <i>P. cf. remotispora</i>). COSTA RICA. San José : 6 km S of Hwy. 2 on Hwy. 12 to Santa María de Dota, 15 Mar. 1986, <i>Yatskievych & McCrary</i> 86-13. Heredia : 2 km SE of Sacramento on Hwy. 114, S slope of Volcán Barva, 18 Mar. 1986, <i>Yatskievych & McCrary</i> 86-31.
<i>P. juglandifolia</i> × <i>macrosora</i>	123I	COSTA RICA. Heredia : 2 km SE of Sacramento on Hwy. 114, S slope of Volcán Barva, 18 Mar. 1986, <i>Yatskievych & McCrary</i> 86-31a.
<i>P. macrosora</i>	41	COSTA RICA. Heredia : 2 km SE of Sacramento on Hwy. 114, S slope of Volcán Barva, 18 Mar. 1986, <i>Yatskievych & McCrary</i> 86-30. MEXICO. Oaxaca : trail to Llano Verde, 1–2 mi. NE of Natividad, 30 Dec. 1983, <i>Yatskievych et al.</i> 83-467; 22 mi. NE of Teotitlán del Camino on rd. to Huautla, 28 Sep. 1986, <i>Yatskievych & Gastony</i> 86-329; (Smith & Mickel, 1977).
<i>P. nobilis</i> var. <i>nobilis</i>	41	MEXICO. México : 1–2 km E of San Rafael on W slope of Volcán Iztaccihuatl, 21 July 1985, <i>Yatskievych et al.</i> 85-211. Oaxaca : 35 km S of Tlaxiaco on Hwy. 125 to Putla, 27 Sep. 1986, <i>Yatskievych & Gastony</i> 86-327; (Smith & Mickel, 1977, as <i>P. nobilis</i>).
var. <i>remotispora</i>	41	MEXICO. Chiapas : ca. 13 km N of Berriozabal, 17 July 1985, <i>Yatskievych et al.</i> 85-186; (Smith & Mickel, 1977, as <i>P. remotispora</i>). Hidalgo : 17 mi. SW of Chapulhuacan on Hwy. 85, 4 May 1983, <i>Yatskievych & Wollenweber</i> 83-128; 32 km SW of Tamazunchale on Hwy. 85 to Jacala, 22 Dec. 1983, <i>Yatskievych et al.</i> 83-353. Veracruz : ca. 3 km SW of Orizaba on Hwy. 150D, Sierra de San Cristobal, 9 May 1983, <i>Yatskievych & Wollenweber</i> 83-158.
<i>P. pumila</i>	82	MEXICO. Chiapas : (Smith & Mickel, 1977). Oaxaca : Llano de Las Flores, at high point on Hwy. 175 N of Ixtlán de Juárez, 13 July 1985, <i>Yatskievych et al.</i> 85-139; NE of Ixtlán de Juárez on old rd. from Capulalpan de Mendez, near junction with newer road to Francisco I. Madero, 19 July 1985, <i>Yatskievych & Gonzalez L.</i> 85-209; (Smith & Mickel, 1977).
<i>P. umbonata</i>	41	MEXICO. Nuevo León : SW of Monterrey on rd. to Valle de San Angel, lower slopes of Mesa de Chipinque, 1 May 1983, <i>Yatskievych & Wollenweber</i> 83-87; km post #29 on Hwy. 58 from Linares to San Roberto, 19 Dec. 1983, <i>Yatskievych et al.</i> 83-299; Cola de Caballo, W of El Cercado, ca. 20 mi. S of Monterrey, 4 Jan. 1984, <i>Yatskievych et al.</i> 84-04; Cañon de San Francisco, Sierra Madre Oriental, ca. 35 km SE of Monterrey, 16 Sep. 1986, <i>Yatskievych & Gastony</i> 86-250. San Luis Potosí : (Mickel et al., 1966). U.S.A. Texas : Brewster Co., Maple Canyon, Basin, Chisos Mtn., 12 Mar. 1985, <i>Yatskievych & McCrary</i> 85-05.

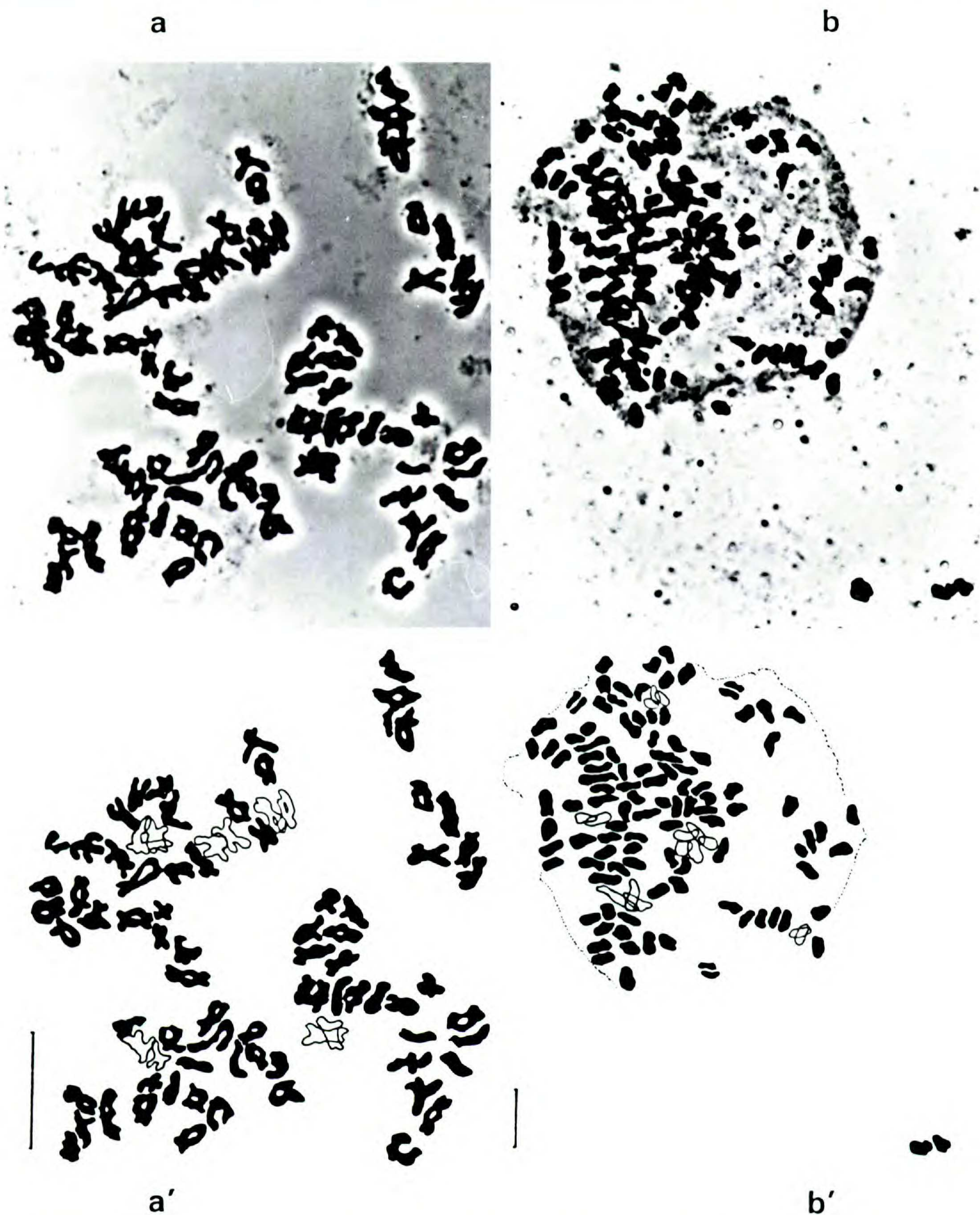


Figure 4. Meiotic preparations illustrating new chromosome counts in *Phanerophlebia*. a, b, photographs; a', b', interpretive camera lucida drawings. —a. *P. juglandifolia*, $2n = 82$ II (Yatskievych & McCrary 86-13). —b. *P. juglandifolia* \times *macrosora*, $2n = 123$ I (Yatskievych & McCrary 86-31a). Scale bars = 10 μ m.

& Mickel, 1977), applies to the rare diploid taxon treated as *P. gastonyi* in the present work, whereas the tetraploid count attributed to *P. cf. remotispora* by Smith and Mickel (1977) applies to the taxon (Fig. 4) treated herein as *P. juglandifolia* sensu

stricto. A further novelty was the documentation of sterile triploid hybrids (Fig. 4) in a mixed population of diploid *P. macrosora* and tetraploid *P. juglandifolia*, the only known primary hybrid in the genus. Thus the cytological situation in this small

group is somewhat more complex than was suggested by earlier studies.

As has been noted above, spore size did not prove to be a reliable indicator of ploidy in *Phanerophlebia* and was useful only in discriminating *P. gastonyi* from its relatives. However, the variability of spores in the small sample of *P. haitiensis* and the apparent high number of malformed spores in this taxon suggest that hybridization and/or polyploidy may have had a role in its formation.

Measurements of epidermal cells were also somewhat equivocal as a means of documenting polyploidy in the genus. Epidermal cells in *Phanerophlebia* species are irregular in size and shape, but are extremely wavy-margined (jigsaw-puzzle-piece shaped) in surface view (Fig. 5). Stomates are restricted to the abaxial surface of the pinnae and are more or less of the polocytic type (sensu Van Cotthem, 1970). Although polyploids, such as *P. pumila*, generally possess larger epidermal cells on both adaxial and abaxial pinna surfaces, the within-sample variation is so high that quantification of these measurements was useless. Measurements of stomates (technically, guard cell lengths) proved to be a more stable means of distinguishing diploid taxa (mean 47.7 μm , range 44.9–54.3 μm) from polyploids (mean 60.8 μm , range 59.6–63.7 μm). Measurements from a cleared pinna of *P. haitiensis* (Fig. 5) fell within the range of guard cell size in polyploid taxa, a further suggestion that this species is a polyploid of some sort.

A brief discussion summarizing what is known about each of the four polyploids in the genus (including *Phanerophlebia haitiensis*), along with speculations as to the likely parentage of each, is presented below. The sterile triploid, *P. juglandifolia* \times *macrospora*, is included in the discussion of *P. juglandifolia*.

Phanerophlebia auriculata. This tetraploid occupies the northwestern portion of the range of the genus (Fig. 6). Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have indicated that it is probably an allopolyploid, but did not result in any firm conclusion regarding potential progenitors within the genus. These data are, however, consistent with the speculations that follow. Analysis of chloroplast DNA restriction site mutations (Yatskievych et al., 1988) suggested that one of its parental species is *P. nobilis*. Morphologically, *P. nobilis* var. *nobilis* and *P. auriculata* are very similar, and the rare occurrence of acroscopically auriculate pinnae in *P. nobilis* (otherwise unique to *P. auriculata*) reinforces this similarity. The other morphologically similar diploid occurring in the northern portion of the generic range is *P. umbon-*

ata (Fig. 6). These taxa all share identical rhizome and petiolar scale types and overall leaf morphology. Specimens from some localities where the ranges of these taxa overlap have been misdetermined by earlier workers and a few samples, such as those collected by Robert Bye in the Sierra Madre of Chihuahua, Mexico (i.e., Bye 6989, 7094, 7363), were quite difficult to determine during the present research. *Phanerophlebia auriculata* and *P. umbonata* share a tendency for rhizomes to branch with age, a feature not seen in *P. nobilis*. Biogeographically, the derivation of *P. auriculata* from *P. nobilis* and *P. umbonata* also seems reasonable, given that these three taxa are the only ones known to occur in northern Mexico. However, mixed populations have not been found in nature.

Phanerophlebia haitiensis. As noted above, measurements of stomata suggest that this rare taxon is some sort of polyploid, and its irregular spore size and relatively high number of malformed spores suggest that hybridization is involved. The irregular pattern of anastomosing venation also leads me to suspect that it is of hybrid origin. This taxon is presumed extinct in Haiti (see below, under taxonomic treatment) and was unavailable for laboratory study, so no comparative information is available from cytological, isozymic, or chloroplast genomic studies. What is unusual is that no other species of *Phanerophlebia* has ever been recorded from Hispaniola, making it difficult to imagine how this taxon might be present at a single, isolated site in Haiti.

Morphologically, *Phanerophlebia haitiensis* is reminiscent of *P. nobilis*. The few specimens that exist are intermediate in venation between free-veined variety *nobilis* and reticulate-veined variety *remotispora*, but *P. haitiensis* has smaller leaves and fewer pinnae than is usual for either variety of *P. nobilis*. It is possible that the irregular spores and reduced leaves might have resulted from inhospitable environmental conditions, rather than from genetic causes, but this would not explain the relatively large stomates and the irregularly anastomosing venation. The existence of two morphologically similar collections from Guatemala (Beaman 3056) and Honduras (Moran 5706) (see under taxonomic treatment) suggests that further fieldwork in southern Mexico and Central America may eventually result in at least partial resolution of the enigma surrounding this taxon.

Phanerophlebia juglandifolia. Yatskievych and Gastony (1987) discussed the two cytotypes constituting the traditional taxon *P. juglandifolia* and ascertained that the type specimen of the name agrees with the tetraploid. Morphological characters

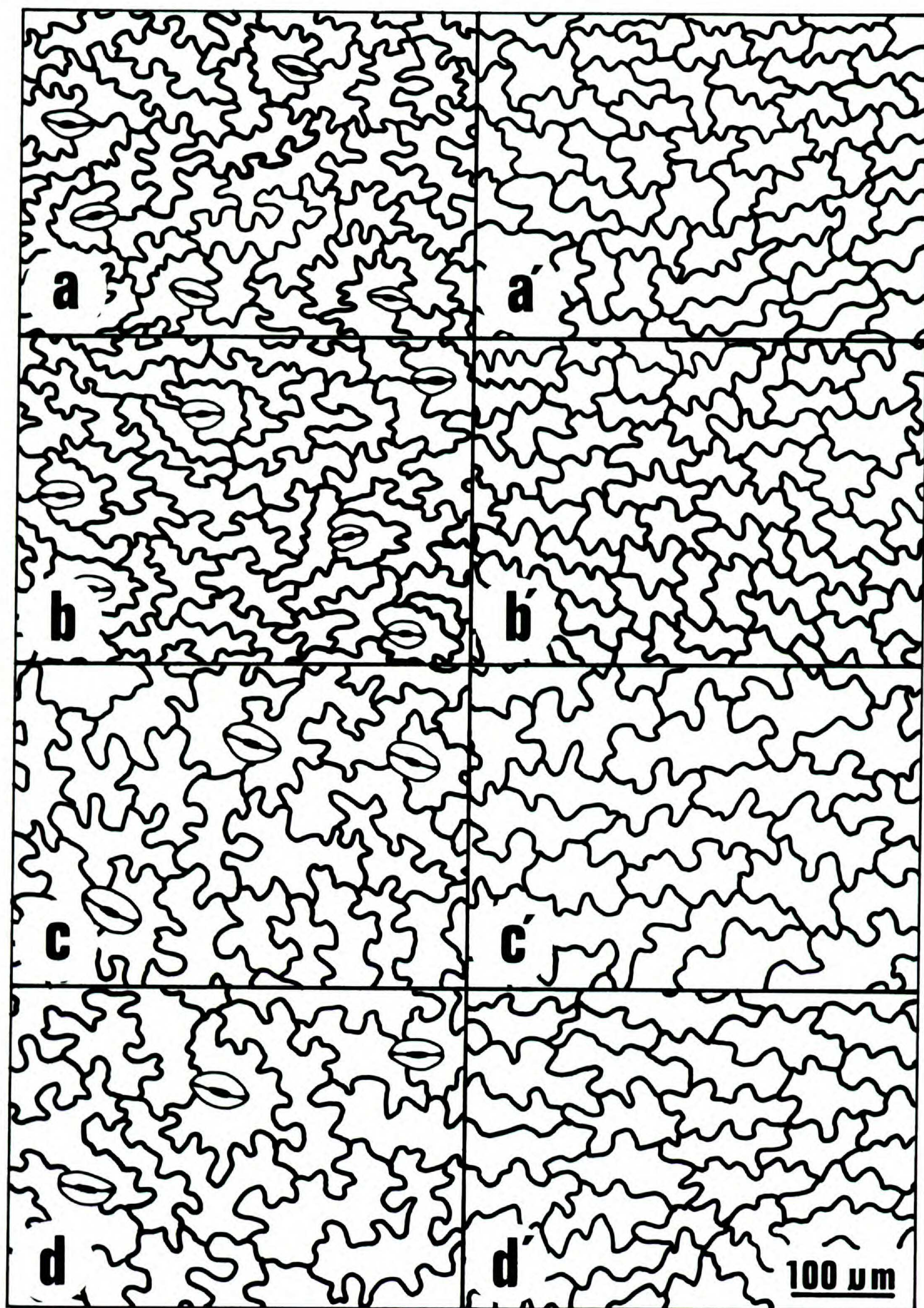


Figure 5. Camera lucida drawings of epidermal cells (surface view) of *Phanerophlebia* species. a–d, abaxial surfaces, with stomates; a'–d', adaxial surfaces. —a. *P. gastonyi* (Yatskievych et al. 85–182). —b. *P. nobilis* var. *remotispora* (Yatskievych & Wollenweber 83–158). —c. *P. pumila* (Mickel 5377). —d. *P. haitiensis* (Ekman 7793).

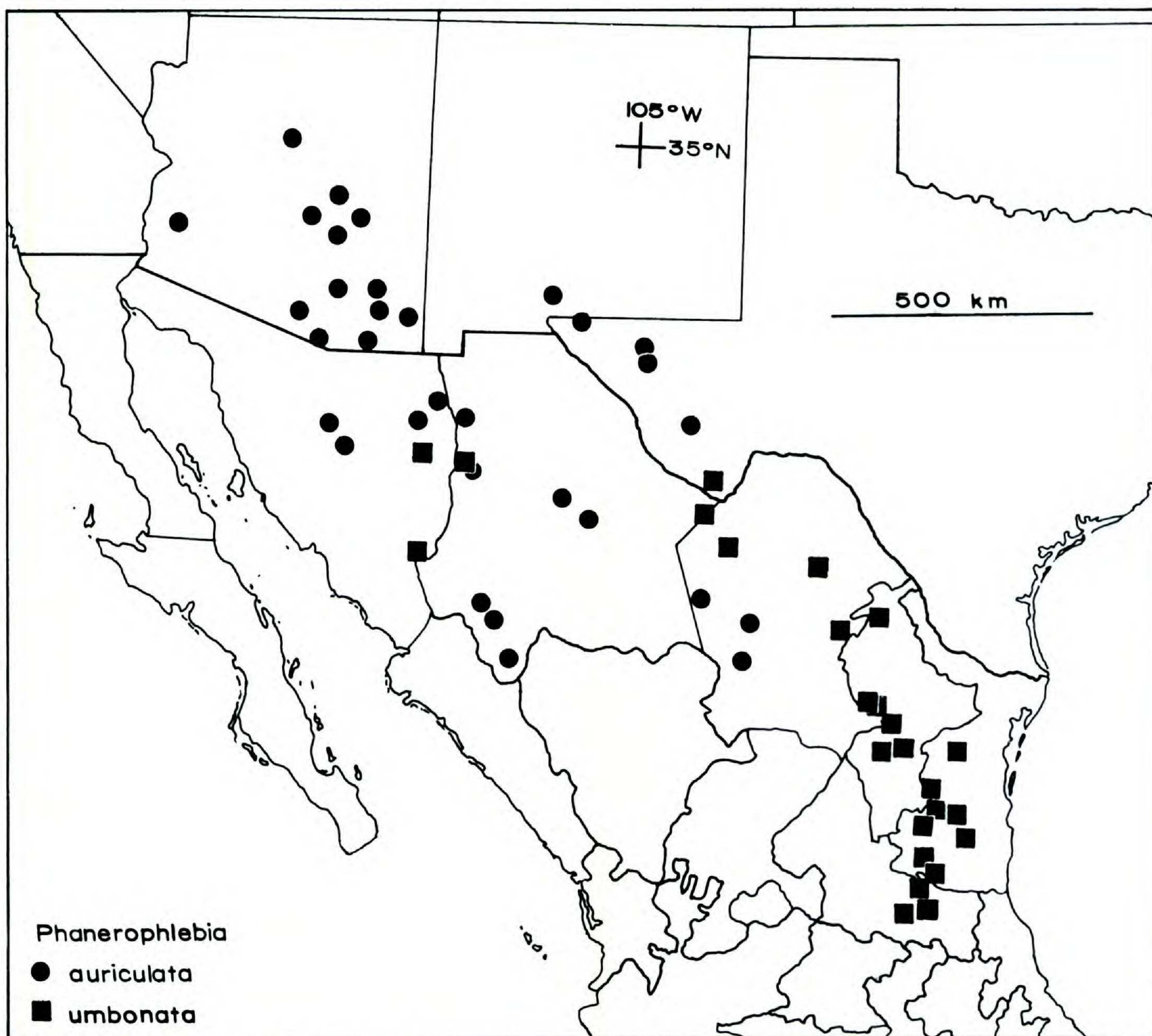


Figure 6. Distributions of *Phanerophlebia auriculata* and *P. umbonata*, based upon herbarium specimens examined.

that separate tetraploid *P. juglandifolia* sensu stricto from the diploid here treated as *P. gastonyi* are detailed below in the taxonomic treatment. Restriction site analysis of the chloroplast genomes (Yatskievych et al., 1988) of these plants confirmed that the diploid plants formerly attributed to the species were a progenitor of the tetraploid. Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) of the tetraploids showed high levels of fixed heterozygosity not segregating in their gametophytic offspring, which is consistent with the hypothesis that these plants are of allopolyploid origin. The identity of the other parental taxon unfortunately remains unclear, particularly because the isozyme studies did not supply convincing evidence for the identity of the second progenitor taxon. The possibilities for the second parent include: (a) *P. nobilis* var. *remotispora*, the other net-veined taxon in the genus; (b) a free-veined taxon, such as *P. macro-*

sora; or (c) a parental taxon that is now either extinct or has not been sampled. Of these three hypotheses, the first, that *P. nobilis* is involved in the parentage of *P. juglandifolia*, seems the least likely. Morphologically, the tetraploids do not combine the critical features of *P. nobilis* and *P. gastonyi*, including rhizome and petiolar scale shape and color and the pattern of spinulose serrulations along the pinna margins. The third hypothesis, of an extinct or at least as yet unsampled progenitor taxon, may be the most likely, but cannot be evaluated from the present data. The other hypothesis, that a free-veined, indusiate species of *Phanerophlebia* contributed the other parental genome to *P. juglandifolia*, was explored by Yatskievych and Gastony (1987). Surprisingly, of the other extant species in the genus, the one that possesses the most likely morphology to account for the differences between *P. juglandifolia* and *P. gastonyi* is *P. macrosora*.

The tetraploid possesses rhizome and petiolar scales with color, shape, and size somewhat intermediate between *P. gastonyi* and *P. macrosora*, and its pinna size, shape, and number are also plausible for this cross (Yatskievych & Gastony, 1987; see also below, under taxonomic treatment). However, *P. juglandifolia* bears a far closer superficial resemblance to *P. gastonyi* than to *P. macrosora*, and lacks the pronounced odor, coarsely serrate pinna margins, and geniculate petiolar bases that characterize the latter species.

Compounding the problem of establishing the parentage of *Phanerophlebia juglandifolia* is the existence of rare, naturally occurring, triploid hybrids between this species and *P. macrosora* (Table 1, Fig. 4) from Costa Rica (see also below, under taxonomic treatment). These hybrids, which produce aborted spores and are therefore sterile, are of intermediate morphology between *P. juglandifolia* and *P. macrosora* and were relatively common at the single site where I was able to observe them. If tetraploid *P. juglandifolia* contained one genome from *P. gastonyi* and the other from *P. macrosora*, then the Costa Rican hybrids would represent a backcross and should display 41 bivalents and 41 univalents at diakinesis. Instead, the triploids display 123 univalents (Table 1). Unfortunately, this weakens the argument that *P. macrosora* might have been the second progenitor of *P. juglandifolia*. The derivation of this tetraploid thus remains unresolved.

Phanerophlebia pumila. This morphologically reduced tetraploid remains enigmatic. Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) indicate that it is probably of allopolyploid origin, as are other tetraploids in the genus, but do not assist in determining its parentage. Surprisingly, its pattern of chloroplast DNA restriction fragments (Yatskievych et al., 1988) do not support any of the extant species of *Phanerophlebia* as a likely progenitor. Thus, the experimental evidence suggests that one or even both parental diploids of this taxon are either extinct or so rare as not to have been sampled by collectors thus far. Potential progenitors are to be sought in the mountains of southern Mexico and adjacent Guatemala, where overall species diversity within the genus is the highest.

The Wagner parsimony analysis of the molecular data (Yatskievych et al., 1988) grouped *Phanerophlebia pumila* and *P. umbonata* as sister taxa. It therefore suggested that the latter species might be involved in the parentage of *P. pumila*. This seems unlikely biogeographically, because the two are widely allopatric. *Phanerophlebia pumila* displays none of the critical morphological features of *P. um-*

bonata, such as a tendency for branching rhizomes or umbonate indusia. Instead, based upon a qualitative assessment of morphological characters, it seems at least plausible that *P. nobilis* might rather have contributed one of the genomes to form *P. pumila*. Although the leaves of *P. pumila* tend to be highly reduced in size and pinna number, and the petiolar scales are at most linear-filiform, the pinna shape and the rhizome scales, as well as the overall leaf shape, suggest some depauperate samples of *P. nobilis*. Further, this diploid can sometimes occur in sinkholes and other habitats normally associated with *P. pumila*, and one set of replicate herbarium specimens examined during this study (Hinton 12428) consisted of a mixed collection of these two species. No other species of *Phanerophlebia*, except the northern tetraploid, *P. auriculata*, has been found in the specialized habitat type (sheltered, overhanging rock walls) to which *P. pumila* is restricted.

PHYLOGENETIC RELATIONSHIPS

Most modern systematists agree that questions of phylogeny are best approached through consideration of the shared, derived characters (synapomorphies) present in various subsets of species within a clade. Such analyses require several assumptions to be accepted. First, the group in question should be monophyletic. Second, it is assumed that character states for various features can in some way be polarized; that is, that there is a rational way to distinguish apomorphies (derived character states) from plesiomorphies (primitive character states). Finally, the researcher must assume that he or she can detect homoplasy (parallel or convergent evolution), which will tend to confuse interpretation of any analysis.

There is little doubt that the species of *Phanerophlebia* are monophyletic. However, the species are so character-poor that although autapomorphies (derived characters unique to one taxon) allow separation of the species from one another, as in the key to species below, there are virtually no synapomorphies that can be documented. Further, those character states that are shared by two or more taxa, such as the rhizome and petiolar scale type of *P. nobilis* and *P. umbonata* (among the diploids), are not easily polarized. Also, it is apparent from study of independent data sets (such as restriction site analysis of the chloroplast genomes) that some characters judged by most earlier workers to be important for classification in the group, particularly the anastomosing venation patterns of *P. gastonyi* and *P. nobilis* var. *remotispora*, are homoplasious.

Thus, no formal cladistic analysis of morphological characters is attempted here.

GENERIC CONSIDERATIONS

The genus *Phanerophlebia* was first erected by Presl (1836), based on *Aspidium nobile* Schltdl. & Cham. Presl (1836) also described *Amblia*, based on *Polypodium juglandifolium* Humb. & Bonpl. ex Willd., and *Cyrtomium*, based on *Polypodium falcatum* L. f. As with many of Presl's genera, acceptance of these innovations was neither immediate nor unanimous, and various authors have treated the groups differently up to present times. Smith (1842) first submerged *Amblia* (which Presl had allied with *Polypodium* L.) in *Phanerophlebia* (which Presl had allied with *Aspidium* Sw.), while maintaining this genus separate from *Cyrtomium*, and recognizing the relationship of both to *Polystichum* Roth. Moore (1857) was the first to unite *Phanerophlebia* and *Cyrtomium*, under the latter name, but retained two subgroups based on the two genera. Diels (1899) presented the most extreme alternative to Presl's segregate genera by submerging *Amblia*, *Cyrtomium*, and *Phanerophlebia* in his large and heterogeneous version of *Polystichum*. Since that time, most pteridologists have either maintained *Phanerophlebia* as a separate genus (e.g., Underwood, 1899; Maxon, 1912) related to *Polystichum*, or have included *Phanerophlebia* in an expanded concept of *Cyrtomium* (e.g., Morton, 1957; Tryon & Tryon, 1982).

No recent workers have questioned the close relationship of *Phanerophlebia* and *Cyrtomium* to *Polystichum*. In fact, one New World taxon, *Polystichum dubium* (Karsten) Diels, of Andean South America and adjacent Central America, continues to be placed in *Cyrtomium* by some authors (e.g., Tryon & Stolze, 1991). Although superficially similar to some *Cyrtomium* and *Phanerophlebia* species, this morphologically variable taxon does not appear to be a geographically disjunct member of either group, and is known to hybridize with *Polystichum platyphyllum* (Willd.) C. Presl in Ecuador (Barrington, 1985). Its classification within *Polystichum* was beyond the scope of the present work, and it remains to be studied in greater detail in the future.

Two hypotheses have been suggested to account for the presence of two morphologically similar "splinter genera" in the Old and New Worlds. Christensen (1930) regarded *Phanerophlebia* and *Cyrtomium* as independent derivatives from different polystichoid ancestors. By this reasoning, the strong similarities between the two groups would reflect convergent evolution, i.e., homoplasy. In contrast, Copeland (1947) suggested a single, Asi-

atic origin for the entire group, with an American component having become established via a transoceanic, disjunctive event. He noted that such a major disjunctive pattern exists in a few other fern genera, such as *Plagiogyria* (Kunze) Mett. (Plagiogyriaceae), and this scenario is therefore plausible.

Evidence in support of Christensen's (1930) hypothesis comes from several sources. An interesting general observation concerns the distribution of apogamous taxa in the polystichoid ferns. Several authors have remarked on the exceedingly large number of apomictic taxa that have been described in *Cyrtomium* (e.g., Shing, 1965) and *C. falcatum* was the subject of classic studies on the phenomenon of apogamy in ferns (Manton, 1950). Examination of the scant information available on apogamy in Asiatic *Polystichum* (Tsai & Shieh, 1985) indicates that this phenomenon also occurs in scattered species within the Asiatic component of the genus. In contrast, as noted above, all fertile taxa of *Phanerophlebia* reproduce sexually. This is also true of all species of American *Polystichum* that have been examined. Although hybridization and polyploidy are relatively common throughout *Polystichum*, apomixis is expressed only in the Old World contingent.

The morphological innovations said to unite *Phanerophlebia* and *Cyrtomium* do not survive close scrutiny. Mitsuta (1977), who studied venation patterns in polystichoid ferns, noted that the areolae in *Phanerophlebia* were narrower (i.e., elongate, with more acute ends) than those in *Cyrtomium* and lacked well differentiated, free, included veinlets as are found in most species of the latter group. Wagner (1979), in a summary of reticulate veins as systematic characters, also noted that the pattern of anastomoses develops differently in the two genera. In *Phanerophlebia*, anastomoses are of a submarginal ontogenetic type, which Wagner (1979) termed "discal," but in *Cyrtomium* they are "costal" in origin.

Patterns of perispore deposition were said by Tryon and Tryon (1982) to be identical in *Phanerophlebia* and *Cyrtomium*. Superficially, the two groups appear similar, but in *Phanerophlebia* species the surface between the inflated folds is smooth to rugulose and imperforate. However, in the seven species representing *Cyrtomium* that I studied, the outer perispore surfaces were not only rugulose, but also had few to many microperforations (Fig. 7).

Other evidence for the separate origins of *Phanerophlebia* and *Cyrtomium* comes from a phylogenetic analysis of restriction site mutations in the chloroplast genomes of the two genera (Yatskievych

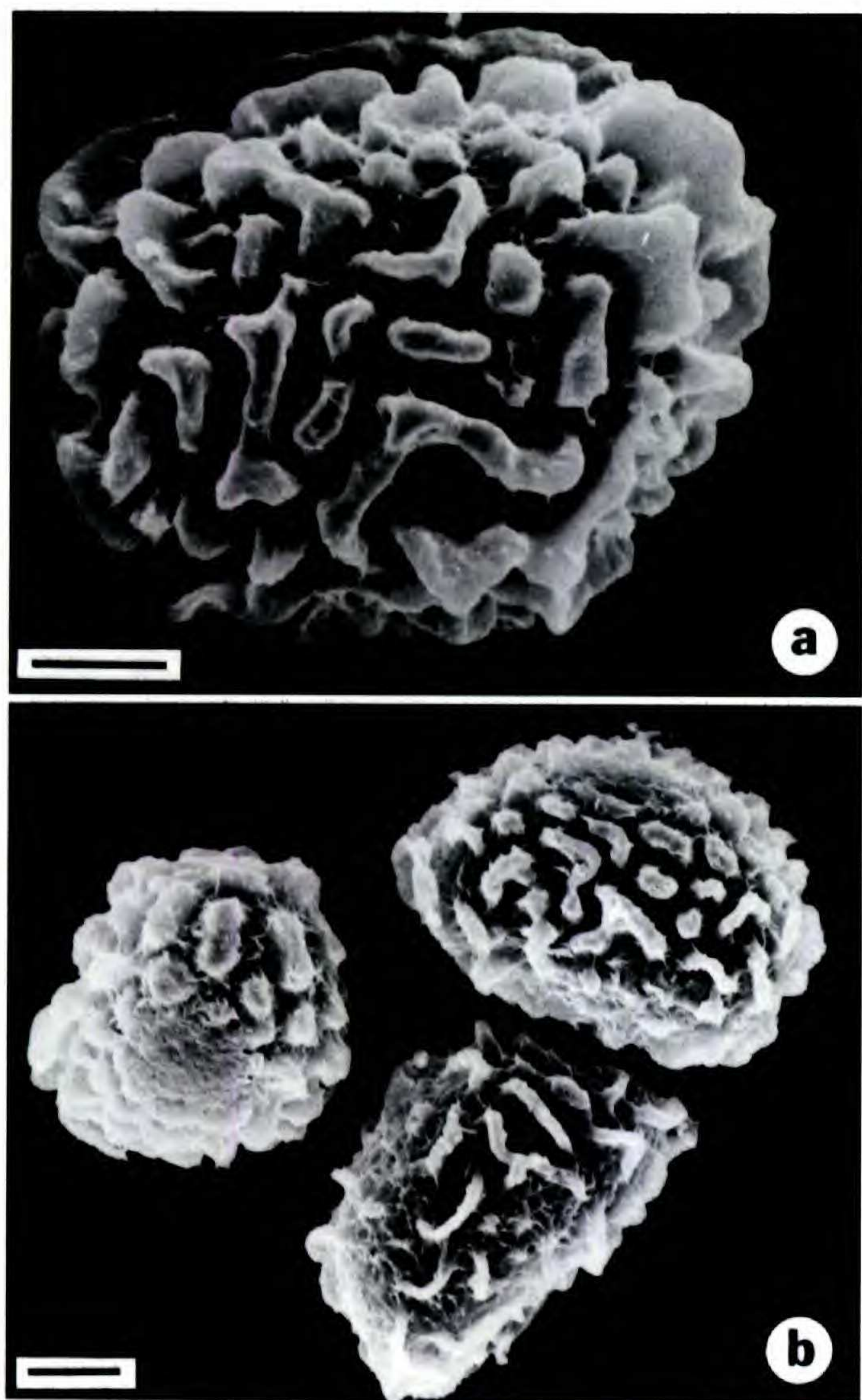


Figure 7. Spores of *Cyrtomium* species. —a. *C. macrophyllum* (Mitsuta s.n.), with the very few microperforations between the folds not easily seen. —b. *C. falcatum* (Yatskievych & McCrary 83–184), the microperforations more easily seen. Scale bars = 10 μ m.

et al., 1988). In that study, the groups of *Phanerophlebia* and *Cyrtomium* species were less related to one another than either was to a group of taxa representing *Polystichum*.

Although present evidence supports the hypothesis that *Phanerophlebia* and *Cyrtomium* were independently derived from different ancestral groups, the real question that remains unanswered is whether either of these derivatives is distinct enough to merit recognition as a genus separate from *Polystichum* (Wagner, 1985). Yatskievych (1989) suggested that simplification of leaf dissection is a trend that has occurred repeatedly in different species groups throughout *Polystichum*. Taken singly, all of the characters said to separate *Phanerophlebia* or *Cyrtomium* from *Polystichum* also occur in other species of that genus.

The venation patterns in two other Asiatic segregates of *Polystichum*, *Cyrtogonellum* Ching and *Cyrtomidictyum* Ching, actually resemble those of

Phanerophlebia far more closely than do those of *Cyrtomium*. However, Ching (1938, 1957) clearly differentiated these segregate genera from *Phanerophlebia*, *Cyrtomium*, and *Polystichum*, based on other morphological innovations they possess. Species in both groups also have been submerged in *Polystichum* by some subsequent authors (e.g., Kramer et al., 1990).

Perispore pattern was cited by Tryon and Tryon (1982) as a stable character for separation of *Cyrtomium* (including *Phanerophlebia*) from *Polystichum*. These authors felt that the simpler, imperforate perispore lacking columellae of *Cyrtomium* was more like that found in *Dryopteris* than the perforate or reticulate, often columellate formation characteristic of *Polystichum*. Although the perispores found in *Cyrtomium*, *Phanerophlebia*, and *Dryopteris* are remarkably similar, two factors argue against placing too much emphasis on this interpretation. First, as noted above, at least some species of *Cyrtomium* possess a perispore with microperforations (Fig. 7). Second, *Polystichum* contains species with a broad range of perispore types. Mitui (1973) attempted to classify the perispore types found in 40 species of *Polystichum*. He differentiated eight perispore types, based on differences in patterns of ornamentation. Most of the species studied had reticulate or perforate perispores of varying complexity, but a small group possessed what Mitui felt to be a derivative perispore type closely related to that of *Cyrtomium* (Figs. 7, 8).

Polystichum species with imperforate perispores are apparently present in both the Old World and New World, although few American taxa have been examined in detail. For example, the perispore type found in *Polystichum lemmonii* Underw. (Fig. 8), of the western United States, is quite similar to that of *Phanerophlebia* species in its relatively compact, imperforate outer layer. As noted above, the widely scattered papillae on the inner perisporeal layer of *Phanerophlebia* species also may represent reduced remnants of earlier columellae. Further studies involving a large number of tropical American species of *Polystichum* are needed to resolve the present ambiguities in our knowledge of perispore evolution in the group.

It is probable that *Phanerophlebia* and *Cyrtomium* will eventually be resubmerged in *Polystichum*. In a phylogenetic sense, recognition of these and other splinter genera results in a paraphyletic *Polystichum*, a situation clearly to be avoided. The decision to continue treating *Phanerophlebia* as a separate genus in the present work was a difficult one and stems from my hesitancy in resubmerging a clearly monophyletic unit back into the poorly re-

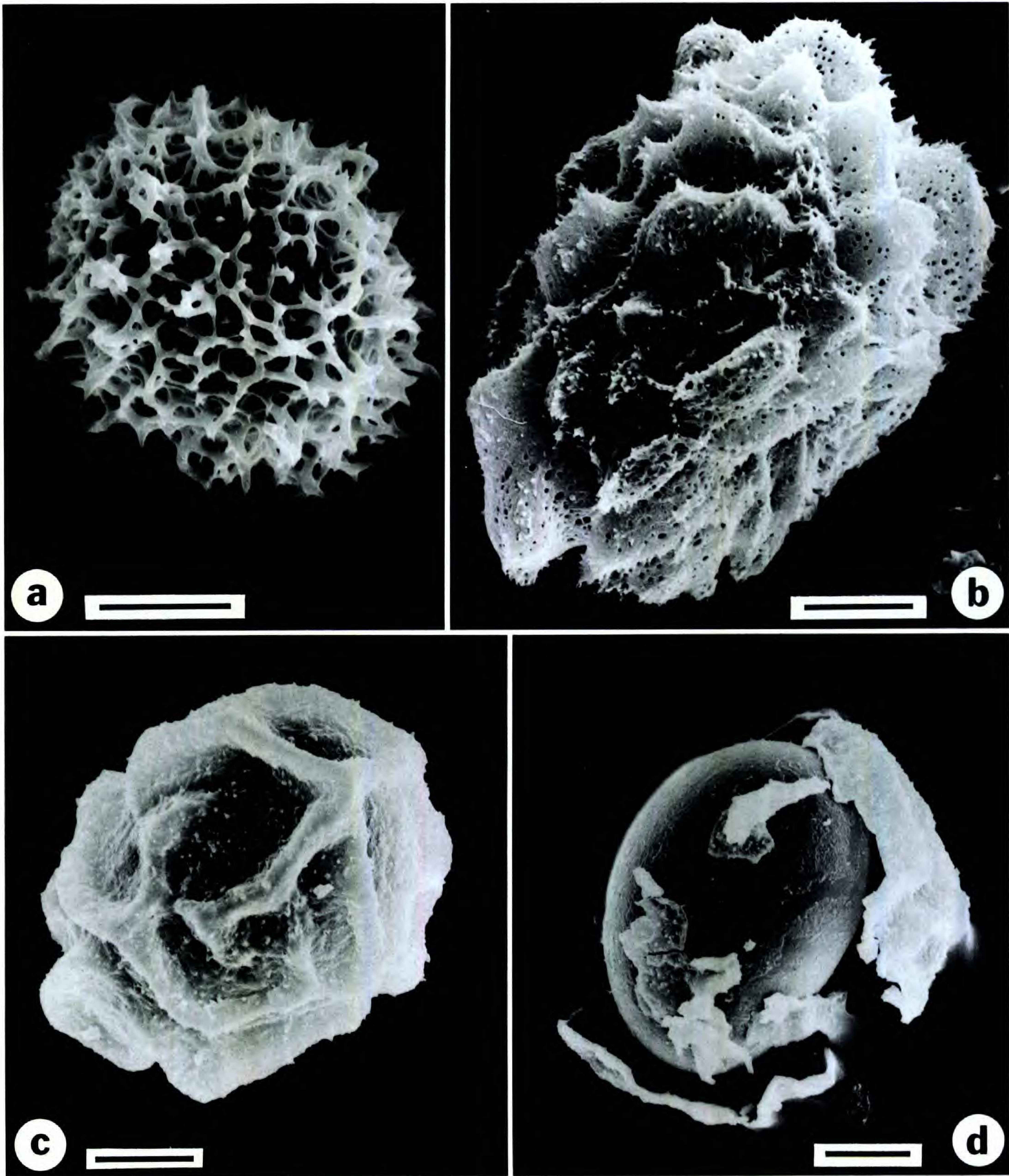


Figure 8. Spores of *Polystichum* species. —a. *P. lonchitis* (Darrow *et al.* 2482), showing the reticulate perispore commonly associated with the genus. —b. *P. munitum* (Yatskievych & McCrary 84–126), with a cristate-microperforate perispore. —c. *P. lemmonii* (D’Arcy 2686), with a perispore type similar to that found in *Phanerophlebia* and *Cyrtomium*. —d. *P. lemmonii* (D’Arcy 2686), abraded spore, showing smooth exine, rugulose inner perispore, and outer perispore with inflated folds. Scale bars = 10 μ m.

solved quagmire that represents our present, limited knowledge of classification in *Polystichum*. Particularly in tropical America, *Polystichum* comprises a diversity of species clusters whose interrelationships have not been studied in detail. We not only do not know which of these species clusters is most closely related phylogenetically, or even morphologically, to the *Phanerophlebia* cluster, but we do not have a clear idea how to polarize the states for the various morphological and other characters separating these groups. Because no stable infrageneric classification, similar to that of

Daigobo (1972) for Japan, presently exists for the New World species, it seems most prudent to avoid publishing the new combinations necessary to incorporate all of the presently recognized taxa of *Phanerophlebia* into *Polystichum*.

TAXONOMIC TREATMENT

Phanerophlebia C. Presl, Tent. Pterid. 84, 1836.

TYPE: *Phanerophlebia nobilis* (Schltdl. & Cham.) C. Presl (*Aspidium nobile* Schltdl. & Cham.).

Amblia C. Presl, Tent. Pterid. 184, 1836. TYPE: *Amblia juglandifolia* (Humb. & Bonpl. ex Willd.) C. Presl [= *Phanerophlebia juglandifolia* (Humb. & Bonpl. ex Willd.) J. Sm.].

Plants perennial, often long-lived, terrestrial, sometimes growing from soil pockets in rock crevices, or epipetric on rock faces; rhizomes dictyostelic, scaly, short-repent to erect, sometimes branched at maturity, usually covered with persistent petiole bases and adventitious roots; rhizome scales unevenly ciliate, the cilia sometimes shed during maturation; leaves clustered at apex of rhi-

zome, monomorphic, evergreen; petioles shorter than or sometimes longer than laminae, scaly (the scales sometimes shed at maturity), with 4–8 vascular bundles arranged in a ring; laminae 1-pinnate (rarely simple) with conform terminal pinnae, chartaceous to subcoriaceous; rachises and costae usually somewhat scaly with reduced scales, grooved adaxially, the grooves \pm confluent at junctions; pinnae asymmetrically subcordate to cuneate at base, sometimes with an acroscopic, basal auricle, spinulose-serrulate along margin, at least distally, ovate to narrowly lanceolate, often somewhat falcate, lacking trichomes, but with reduced, often hairlike scales along veins (these grading into the broader, more typical scales along the rachis and petiole); venation anadromous (this often difficult to observe), pinnate, the veins 1–4-branched, extending \pm to margin, free or with 1–3 series of marginal anastomoses; sori terminal or apparently lateral on veins, round, in (1–)2–4 series between costa and margin; indusia absent or present, if present then peltate, with erose margins, persistent at maturity or fugacious; sporangia with 64 spores; spores monolet, dark brown; perispore with prominent, inflated folds; exospore smooth. Chromosome number: $x = 41$.

KEY TO THE TAXA OF *PHANEROPHLEBIA*

(the rare, sterile hybrid, *P. juglandifolia* \times *P. macrosora* is not included, but may key imperfectly to one of its parents)

- 1a. Veins commonly anastomosing toward the margins, in 1–3 series (less frequent in *P. haitiensis*), these sometimes distributed irregularly.
 - 2a. Sori indusiate (the indusium shriveling at maturity or fugacious); rhizome and petiole scales concolorous, reddish brown.
 - 3a. Lateral pinnae (2–)6–17 pairs; pinna margins spinulose-serrulate nearly to base 6b. *Phanerophlebia nobilis* var. *remotispora*
 - 3b. Lateral pinnae 2–4 pairs; pinna margins spinulose-serrulate only in distal half 3. *Phanerophlebia haitiensis*
 - 2b. Sori exindusiate; rhizome and petiole scales bicolorous, with darker, sclerotic centers and lighter margins.
 - 4a. Petiolar scales not overlapping, 4–6 mm long, with broad, dark, sclerotic centers and narrow, hyaline margins; buds absent; spores 30–42 μ m long 2. *Phanerophlebia gastonyi*
 - 4b. Petiolar scales usually overlapping, 6–11 mm long, with dark brown central stripes and lighter margins of about equal width; buds often present on rachis in axils of distal pinnae; spores 41–60 μ m long 4. *Phanerophlebia juglandifolia*
- 1b. Veins free, or with a few, rare anastomoses.
 - 5a. Lateral pinnae 0–3(–5) pairs; leaves usually <40 cm long; broadest petiolar scales <2 mm wide 7. *Phanerophlebia pumila*
 - 5b. Lateral pinnae (2–)5–17 pairs; leaves usually >40 cm long; broadest petiolar scales >2 mm wide.
 - 6a. Petiolar scales stramineous to tan; leaves to 2.7 m long; rhizome scales 10–15 mm long, 5–7 mm wide; plants with an unpleasant, skunklike odor when fresh 5. *Phanerophlebia macrosora*
 - 6b. Petiolar scales brown or reddish brown (rarely lighter colored with age); leaves to 1.25 m long; rhizome scales 2.5–7.5 mm long, 1–4 mm wide; plants without an unpleasant, skunklike odor when fresh.
 - 7a. Indusia not shriveled at maturity, \pm persistent, with a raised, central projection (umbo) 8. *Phanerophlebia umbonata*
 - 7b. Indusia shriveled at maturity, often fugacious, flat to concave centrally, not umbonate.
 - 8a. At least some pinnae with a prominent, acroscopic auricle at base; plants of sheltered soil pockets in rock crevices and ledges of mesic canyons; SW United States to N Mexico 1. *Phanerophlebia auriculata*
 - 8b. Pinnae rarely auriculate at base; plants of stream banks and forest understory (rarely in sinkholes or rock crevices); nearly throughout Mexico in mountainous areas 6a. *Phanerophlebia nobilis* var. *nobilis*

1. *Phanerophlebia auriculata* Underwood, Bull. Torrey Bot. Club 26: 212. 1899. *Cyrtomium auriculatum* (Underw.) C. V. Morton, Amer. Fern J. 47: 54. 1957. TYPE: Mexico. Chihuahua: cool, damp cliffs, Mapula Mountains, 17 Oct. 1886, *Pringle 831* (holotype, NY; isotypes, CAS, F, GH, K, LL, MICH, MO, NY, P, UC, US).

Plants not strongly scented; rhizomes to ca. 15 mm diam., deeply seated in substrate, short-repent to ascending, sometimes branched at maturity; rhizome scales 3.5–7.5 mm long, 1–4 mm wide, ovate to elliptic-lanceolate, ciliate, concolorous, brown (rarely lighter colored with age); leaves 10–60(–75) cm long (very short leaves sometimes fertile); petioles shorter than to nearly as long as laminae; petiolar scales sometimes deciduous, dense and overlapping, much like rhizome scales, the broadest ca. 4 mm wide, grading into reduced, hairlike structures above; pinnae (2–)5–12 pairs, to 9 cm long, ovate to lanceolate, usually falcate, the apex usually attenuate, the base obliquely cuneate to subcordate and usually with a prominent, acroscopic auricle (at least some present on every plant), rarely irregularly incised, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free, 1–3-branched; sori in 2–4 series between costa and margin; indusia 0.6–0.9 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 41–60 μ m long. Chromosome number: $n = 82$.

Illustrations. See original description; also Dittmer et al. (1954: 38), Knobloch and Correll (1962: 164, pinna), Mickel (1979: 163).

Phanerophlebia auriculata grows in soil pockets in rock crevices (usually granite or quartzite); it is restricted to mesic, sheltered ravines and canyons, in oak and pine-oak forests; 600–2300 m; southwestern United States (Arizona, New Mexico, Texas) and northern Mexico (Chihuahua, Coahuila, Sonora) (Fig. 6). Clausen's (1949) report of this species from Nuevo León was based upon misdetermined specimens of *P. umbonata*.

Isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have indicated that *Phanerophlebia auriculata* is an allotetraploid taxon. An examination of chloroplast DNA variation in the genus (Yatskievych, 1988) implicated the diploid *P. nobilis* as one potential parent. Based on morphological characters and distribution, the diploid *P. umbonata* appears to be the most likely extant candidate for the other parent. These three taxa are very similar in details of leaf shape and size, rhizome and petiolar scale shape and coloration, pinna

number, and venation. Sterile specimens of the two presumed parents are virtually indistinguishable morphologically. *Phanerophlebia auriculata* shows no tendency toward umbonate indusia, a distinguishing character of *P. umbonata*, but does have a tendency for branched rhizomes, which are common in *P. umbonata*, but not produced in *P. nobilis*. The acroscopically auriculate pinnae of *P. auriculata* are not found in *P. umbonata*, but can be encountered rarely in *P. nobilis*. Small auricles are also encountered commonly in another tetraploid, *P. pumila*, suggesting that this character may arise as a side effect of the combination of parental genomes giving rise to these allopolyploids.

Representative specimens. U.S.A. **Arizona:** Cochise County, short canyon near mouth of Garden Canyon, Huachuca Mountains, *Goodding 162–50* (ARIZ, MICH); Gila County, SE wall of Parker Canyon, Sierra Ancha, *Windham 0109B* (ASC); Graham County, Aravaipa Canyon, in the "Box" below Klondyke, *Phillips & Reynolds 2946* (ARIZ, CAS, GH, US); Maricopa County, north canyons, Superstition Mountains, *Goodding 6146* (ARIZ); Pima County, near the top and on the N side of Mt. Baboquivari, *Gould, Darrow & Haskell 2788* (ARIZ); Santa Cruz County, Sycamore Canyon, Pajarito Mountains, *T. & M. Van Devender s.n.* (ARIZ); Yavapai County, Boynton Canyon, W of Sedona, *Deaver 4788* (ARIZ, ASC); Yuma County, deep narrow canyon, Kofa Mountains, *Goodding & Hinckley F-9-39* (MICH, US). **New Mexico:** Dona Ana County, Ice Canyon, Organ Mountains, *Worthington 7679* (ARIZ, NY, UTEP); Socorro County, Luna Park Campground, San Mateo Mountains, *Reeves et al. 88-1* (NMC). **Texas:** Culberson County, Victorio Canyon, E margin of Sierra Diablo, *Johnston, Wendt & Chiang C. 10728* (CAS, LL); El Paso County, Hueco Tanks, Hueco Mountains, *Waterfall 6635* (GH, MO, NY); Jeff Davis County, Rose Canyon, 15 mi. N of Alpine, *Warnock 21779* (LL). **MEXICO. Chihuahua:** vicinity of village of Majalca, *Correll & Johnston 21772* (LL, US). **Coahuila:** Cañon de Calabasa, Sierra Mojada, *Stewart 2198* (GH, LL). **Sonora:** Cañon de Bavispe, region of Río de Bavispe, *Phillips 546* (ARIZ, GH, MICH, NY).

2. *Phanerophlebia gastonyi* Yatskievych, Novon 2: 445. 1992. TYPE: Mexico. Chiapas: ca. 13 km NW of Berriózabal, limestone outcrops in evergreen tropical hardwood forest, elevation 1000 m, 15 July 1985, *Yatskievych, González L., Ranker, G. Starr & C. Starr 85–182* (holotype, MO; isotypes, ARIZ, CHAPA, IND, MEXU, NY, UAMIZ, UC).

Plants not strongly scented; rhizomes to ca. 5 mm diam., superficial on substrate, short-repent, not branched at maturity; rhizome scales 2.5–4.5 mm long, 1.5–2 mm wide, ovate to elliptic-lanceolate, ciliate, bicolorous with broad, dark, sclerotic centers and narrow hyaline margins; leaves to 45(–55) cm long; petioles slightly shorter than to usually longer than laminae; petiolar scales usually decid-

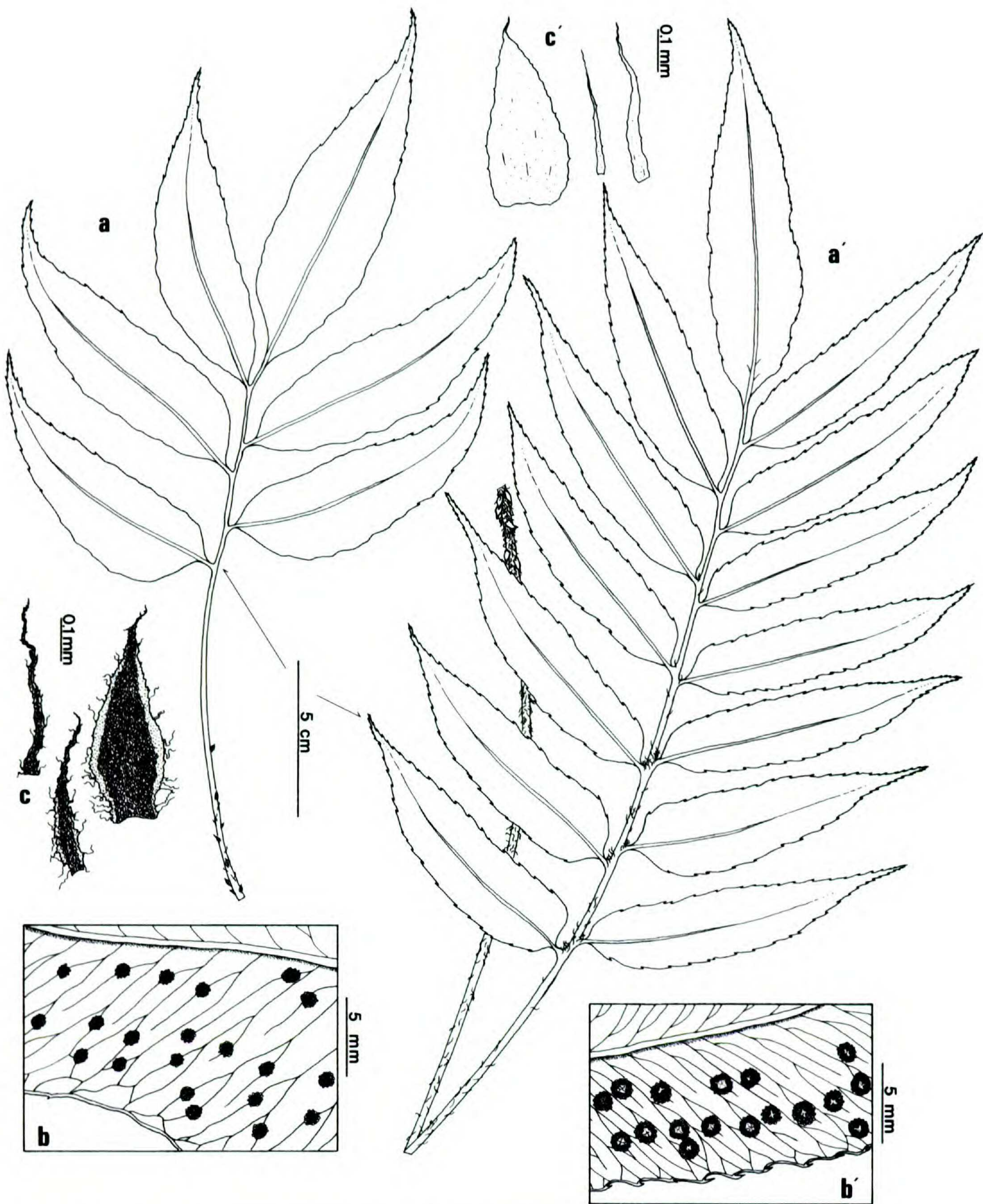


Figure 9. *Phanerophlebia gastonyi* (a–c) and *P. nobilis* var. *remotispora* (a'–c'). —a, a'. Representative leaves. —b, b'. Details of pinnae showing venation, sori, indusia, and pinna margins. —c, c'. Representative series of petiolar scales. (a–c from Yatskievych *et al.* 85–182; a'–c' from Yatskievych 85–186.)

uous with age, mostly not overlapping, much like rhizome scales, the broadest 2 mm wide, the reduced hairlike structures uncommon among the broader scales; pinnae (0–)1–3(–4) pairs, to 12(–15.5) cm long, ovate to lance-ovate, sometimes somewhat falcate, the apex acute to attenuate, the

base obliquely cuneate to rounded, sometimes nearly equilateral, the margins entire to slightly undulate proximally, spinulose-serrulate only in distal half; buds absent from axils of distal pinnae; veins with 1–3 series of regular marginal anastomoses, 2–4-branched; sori in (1–)2–4 series between costa

and margin; sori exindusiate; spores 30–42 μm long. Chromosome number: $n = 41$.

Illustrations. Figure 9a–c; see also Mickel and Beitel (1988: 520, as *P. juglandifolia*).

Phanerophlebia gastonyi grows in moist soil, less commonly on fissured limestone rock faces, in shaded understory of cloud forests and montane rainforests; 900–2200 m; southern Mexico (Chiapas, Oaxaca, Veracruz) (Fig. 10).

Specimens of *Phanerophlebia gastonyi* have been identified by previous workers as *P. juglandifolia*, but molecular studies (Yatskievych et al., 1988) have identified it as a progenitor of that species. The two taxa are very similar morphologically, but can be separated by the characters included in the key. Diploid *P. gastonyi* is treated here at species rank, rather than as a variety or subspecies of *P. juglandifolia*, because isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have suggested that the latter, tetraploid taxon is of allopolyploid origin, with the other diploid parent not yet identified.

Representative specimens. MEXICO. **Chiapas:** 13 km N of Berriózabal, *Breedlove & Smith 21652* (DS, F, MICH, NY). **Oaxaca:** trail from San Pedro Nolasco N to the Llano Verde, *Mickel & Hellwig 3786B* (NY). **Veracruz:** ca. 12 km S of Misantla, *Conant 726* (GH, MEXU).

3. *Phanerophlebia haitiensis* C. Christensen, Kongl. Svenska Vetenskapsakad. Handl. III 16: 42 + pl. 10, figs. 1–4. 1937. *Cyrtomium haitiense* (C. Chr.) C. V. Morton, Amer. Fern J. 47: 55. 1957. TYPE: Haiti. Massif de la Selle, Ganthier, Badeau, deep gulch above Badeau, alt. 2000 m, 28 Jan. 1925, *Ekman 3119* (holotype, S; isotypes, BM, US).

Plants not strongly scented; rhizomes to ca. 10 mm diam., apparently deeply seated in substrate, short-repent to ascending, not branched at maturity; rhizome scales 4.5–7.0 mm long, 2–4 mm wide, ovate to elliptic-lanceolate, erose-denticulate, with few, short cilia at base, concolorous, brown (rarely lighter colored with age); leaves to 50 cm long; petioles slightly shorter than to longer than laminae; petiolar scales usually deciduous, loosely overlapping, much like rhizome scales, the broadest ca. 3 mm wide, grading into reduced, hairlike structures above; pinnae 1–4 pairs, to 9 cm long, lanceolate to lance-ovate, usually falcate, the apex acute to attenuate, the base unevenly cuneate and lacking an acroscopic auricle, the margins sometimes slightly undulate, spinulose-serrulate in distal half; buds absent from axils of distal pinnae; veins with irregular marginal anastomoses, 2–3-branched; sori in 1–2(–3) series between costa and margin; in-

usia 0.7–1.1 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 35–56 μm long, often lacking a well-developed perispore. Chromosome number unknown.

Illustrations. See original description.

Phanerophlebia haitiensis grows on protected limestone cliffs; 2000–2500 m; Central America (Guatemala, Honduras), Haiti (Fig. 10).

This perplexing taxon is apparently of hybrid origin, based on its irregularly sized spores with reduced perispore deposition and its irregularly anastomosing veins. Examination of stomates from a cleared pinna fragment indicates a size range in agreement with polyploid taxa in the genus (see previous discussion). It has not been re-collected in Haiti since Ekman's original specimens (both from the same locality). John T. Mickel (pers. comm.) has searched for this species and failed to locate it. It is therefore presumed extinct there.

Single collections from Guatemala and Honduras (see below and Fig. 10) share with the Haitian collections the irregularly anastomosing venation and spores of variable size with apparently reduced perispore deposition. The Guatemalan collection possesses few mature sporangia, however, and plants at this locality require further study. Smith (1981) suggested affinities between this species and *P. lindenii* E. Fourn., which is here treated as a synonym of *P. pumila* (M. Martens & Galeotti) Fée. See the treatment of the latter species for further discussion.

Specimens examined. HAITI. Massif de la Selle, Croix des Bouquets, ravine between M. Mérillon et M. Badeau, type locality, *Ekman 7793* (F, GH, MICH, NY, US). GUATEMALA. **Huehuetenango:** km 324–325 on Ruta Nacional 9N between Chemal and San Juan Ixcay, Sierra de los Cuchumatanes, *Beaman 3056* (GH, TEX, UC). HONDURAS. **Santa Bárbara:** 7 km N of El Mochito on E slopes of Mt. Santa Bárbara, *Moran 5706* (MO).

4. *Phanerophlebia juglandifolia* (Humboldt & Bonpland ex Willdenow) J. Smith, J. Bot. (Hooker) 4: 187. 1841. *Polypodium juglandifolium* Humb. & Bonpl. ex Willd., Sp. Pl. (ed. 4) 5: 195. 1810. *Amblia juglandifolia* (Humb. & Bonpl. ex Willd.) C. Presl, Tent. Pterid. 185. 1836. *Aspidium juglandifolium* (Humb. & Bonpl. ex Willd.) Kunze ex Klotzsch, Linnaea 20: 363. 1847. *Cyrtomium juglandifolium* (Humb. & Bonpl. ex Willd.) T. Moore, Index Fil. lxxxiii. 1857. *Dryopteris juglandifolia* (Humb. & Bonpl. ex Willd.) Kuntze, Revis. Gen. Pl. 2: 813. 1891. *Polystichum juglandifolium* (Humb. & Bonpl. ex Willd.) Diels in Engler & Prantl, Nat. Pflanzenfam. 1(4): 191. 1899. TYPE: Venezuela. Monagas: Caripe, *Humboldt & Bonpland s.n.* (holotype, B—Herb. Willd. 19688, sheets 1a, 1b; isotypes, P, NY (fragment)).

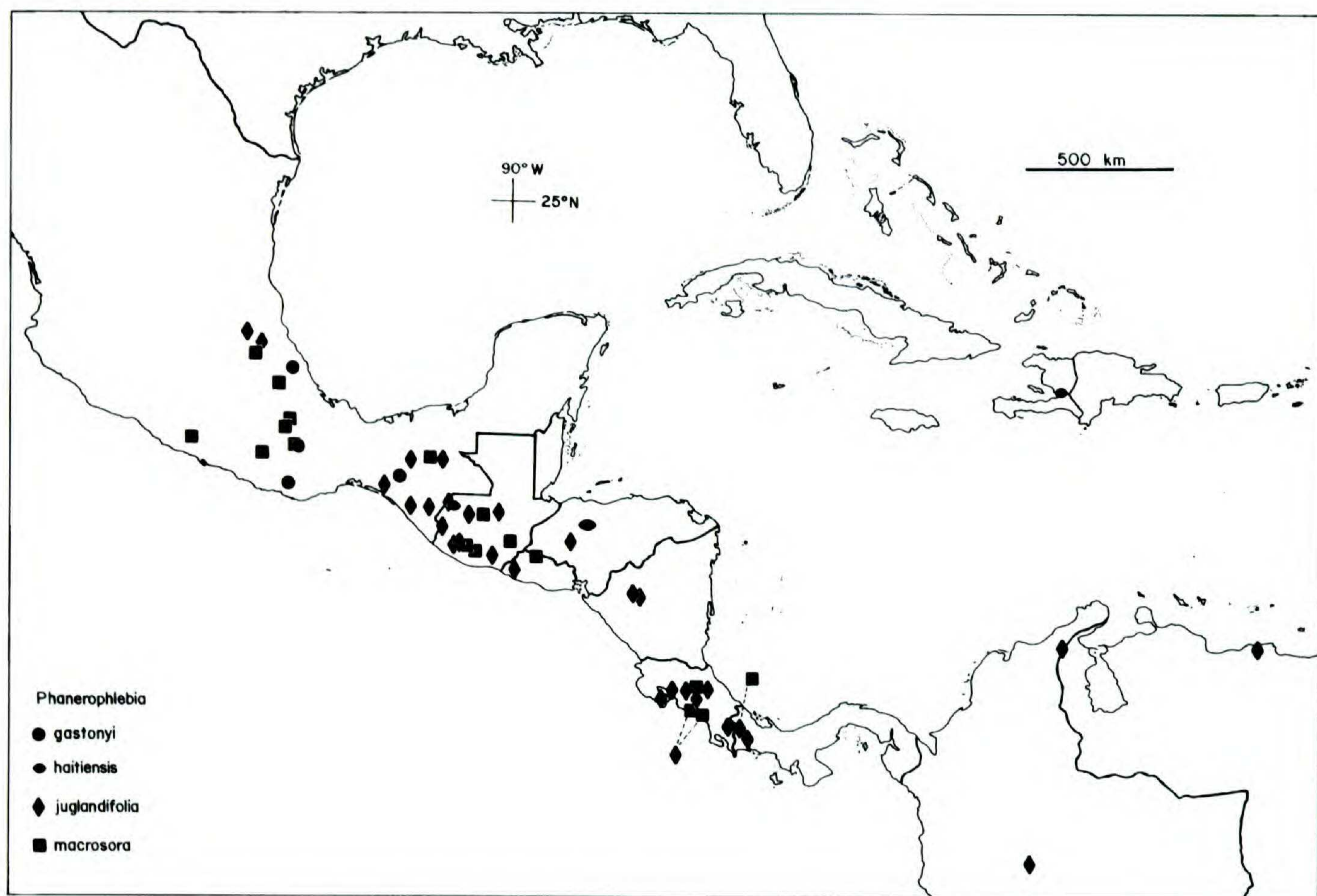


Figure 10. Distributions of *Phanerophlebia gastonyi*, *P. haitiensis*, *P. juglandifolia*, and *P. macrosora*, based upon herbarium specimens examined.

Plants not strongly scented; rhizomes to ca. 7 mm diam., generally deeply seated in substrate (sometimes superficial), short-repent to nearly erect, not branched at maturity; rhizome scales 6.0–10.5 mm long, 3–5 mm wide, lanceolate, ciliate, bicolorous with broad or sometimes narrow, dark brown, somewhat sclerotic centers and hyaline margins as wide as centers or narrower; leaves to 60(–85) cm long; petioles shorter than to slightly longer than laminae; petiolar scales subpersistent, overlapping and often dense, much like rhizome scales, the broadest 4 mm wide, grading into reduced, hairlike structures; pinnae 2–4(–6) pairs, to 17.5 cm long, ovate to lance-ovate, usually somewhat falcate, the apex attenuate, the base obliquely cuneate to rounded, the margins often slightly undulate proximally, spinulose-serrulate in distal half or more commonly in distal two-thirds; buds present on at least some leaves in each population, the gemmae in axils of distal pinnae (rarely in axils of more proximal pinnae); veins with 1–3 series of regular marginal anastomoses, 3–5-branched; sori in 2–4(–5) series between costa and margin; sori exindusiate; spores 41–60 μm long. Chromosome number: $n = 82$.

Illustrations. Humboldt et al. (1825, 7: pl. 665, as *Polypodium juglandifolium*), Underwood (1899:

pl. 359–360, pinna), Vareschi (1969: 368, pinna); Stolze (1981: 166, as *Cyrtomium juglandifolium*).

Phanerophlebia juglandifolia grows in moist soil of ravines and slopes, associated with limestone or volcanic substrate, in rainforests and evergreen cloud forests, rarely in pine-oak forest; (350–)700–2700 m; eastern and southern Mexico (Chiapas and disjunctly in Hidalgo and Veracruz), nearly throughout Central America, to Colombia and Venezuela (Fig. 10).

Previous workers were unaware that *Phanerophlebia juglandifolia*, as traditionally circumscribed, was a heterogeneous mixture of a widespread, allotetraploid taxon (to which the type of this name can be ascribed) and one of its diploid progenitors, which is here treated as *P. gastonyi*. Unfortunately, the identity of the other parental taxon remains unclear. Compounding the problem of morphological circumscription of *P. juglandifolia* was the discovery of rare, naturally occurring hybrids between this species and *P. macrosora*. These hybrids, which are apparently restricted to the mountains of central Costa Rica, are sterile triploids of intermediate morphology, and were relatively commonly encountered in the single site where I was able to observe these plants. They are

morphologically variable, though most are robust plants with the overall aspect of *P. macrosora*. They can be separated from both parents by their somewhat smaller, bicolorous, petiolar and rhizome scales, irregularly anastomosing venation, highly reduced or absent indusia, and malformed spores (many of the sporangia also abort early in their development). The only specimens seen that represent this hybrid are both from medium elevations (1700–2000 m) in the volcanic mountains of central Costa Rica (Alajuela, La Ventolera, on S slope of Volcán de Poás, *Standley 34531* (GH, US); Heredia, 2 km SE of Sacramento on hwy. 114 from San José de la Montaña, S slope of Volcán Barva, *Yatskievych & McCrary 86–31a* (CR, IND, MO, NY)).

Representative specimens (of *P. juglandifolia*). MEXICO. **Chiapas:** above Finca Cuxtepec, mpo. Angel Albino Corzo, *Breedlove & Strother 46731* (CAS). **Hidalgo:** 8–9 km N de Ismolintla, mpo. Molango, *Hernández M., Cortés & Hernández M. 5916* (MEXU, MO). **Veracruz:** hacia el arroyo Toluca, desde la vereda que va a Tzimentey, mpo. Huayacocotla, *Palma G. 67* (XAL). GUATEMALA. **Alta Verapaz:** trail between Sepacuité and Secaquim, *Maxon & Hay 3289* (US). **El Quiché:** mountain slopes S of Nebaj, *Proctor 25075* (DS, LL, TEX, US). **Escuintla:** between Santa María de Jesus and Palín, *Standley 61300* (F). **Huehuetenango:** above San Juan Ixcay, Sierra de Cuchumatanes, *Steyermark 50036* (F, US). **Quetzaltenango:** along road between La Finca Pirineos and Patzulín, *Standley 87078* (F, US). **San Marcos:** 1 mi. above Africa, ca. 3.3 mi. above Finca Armenia above San Rafael, *Croat 40940* (MO). EL SALVADOR. **Santa Ana:** NE slope of Cerro de los Naranjos, *Tucker 1288* (BH, GH, K, LL, MICH, NY, US). HONDURAS. **Lempira:** Celaque National Park, trail from Camp 1 to Río Naranjal, *Moran 5565* (MO). **Santa Barbara:** Cerro Santa Barbara, 10 km E de Lago Yojoga, *Clewell & Hazlett 3975* (MO). NICARAGUA. **Matagalpa:** Valle Palcila, *Moreno 7014* (MO). **Jinotega:** Cerro Ciale, SW of Jinotega, *Standley 10468* (F, US). COSTA RICA. **Alajuela:** Tapesco de Lacero, Alfaro Ruiz, *Smith 1463* (GH, NY). **Cartago:** Carpintera, *Brade & Brade 53* (GH). **Heredia:** Porrosatí de Barva, *Gómez 22207* (CR). **Puntarenas:** Monte Verde, around community along Río Guacimal below Lechería, *Hammel & Trainer 13825* (MO). **San José:** along Quebrada Tablazo and on forested slope above creek, NE part of Altos Tablazo, *Grayum & Schatz 5166* (MO). PANAMA. **Chiriquí:** 12 mi. from Gualaca on road to Cerro Hornito, *Antonio 1752* (MO). VENEZUELA. **Distrito Federal:** Cerro de Avila, Quebrada Chacaito, *Manara s.n.* (MO). COLOMBIA. **Cundinamarca:** Salto de Tequendam, Bogotá, *Voyage de J. Triana 61* (P). **Magdalena:** Sierra de Perijá, 10 km ENE of Manure, 3 km from Venezuelan border, *Grant 10799* (GH).

5. *Phanerophlebia macrosora* (Baker) Underwood, Bull. Torrey Bot. Club 26: 213. 1899. *Aspidium juglandifolium* (Humb. & Bonpl. ex Willd.) Kunze ex Klotzsch var. *macrosorum* Baker, J. Bot. 25: 25. 1887. *Cyrtomium macrosorum* (Baker) C. V. Morton, Amer. Fern J. 47: 55. 1957. TYPE: Costa Rica. Without further locality, 1886(?), *Cooper s.n.* (holotype, K; isotypes, GH, NY (fragment), US).

Phanerophlebia guatemalensis Underw., Bull. Torrey Bot. Club 26: 214. 1899. TYPE: Guatemala. Quiché: San Miguel Upsantán, alt. 7000 pp., Apr. 1892, *Heyde & Lux s.n.* [herb. J. Donnell-Smith 3241] (holotype, NY; isotypes, GH, P, US).

Plants with a strong, unpleasant, skunklike odor when fresh; rhizomes to ca. 20 mm diam., deeply seated in substrate, erect or ascending, unbranched at maturity; rhizome scales 10–15 mm long, 5–7 mm wide, ovate to lance-ovate, erose-ciliate, concolorous (rarely with a slightly darkened central area); leaves 0.7–2.7 m long; petioles shorter than to nearly as long as laminae; petiolar scales persistent, dense and overlapping, much like rhizome scales, the broadest ca. 7 mm wide, mixed with reduced, hairlike structures above; pinnae (4–)6–17 pairs, to 27 cm long, narrowly oblong-lanceolate, occasionally slightly falcate, the apex attenuate, the base obliquely cuneate to rounded and lacking an acroscopic auricle, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free, 3–4-branched; sori in 2–4 series between costa and margin; indusia 0.6–1.1 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 41–60 μm long. Chromosome number: $n = 41$.

Illustrations. Smith (1981: 330), Stolze (1981: 166, as *Cyrtomium macrosorum*), Mickel and Beitel (1988: 520).

Phanerophlebia macrosora grows in moist soil in mesic ravines and on shaded slopes, usually with igneous or volcanic substrate, in montane rainforests and cloud forests, rarely in oak forests; 1800–3200 m; eastern and southern Mexico (Chiapas, Hidalgo, Oaxaca, Veracruz), through Central America, to western Panama (Fig. 10).

This interesting species is easily recognized by its large, coarsely divided, brittle leaves with a thick, coriaceous texture, by its densely and persistently scaly petioles, and by its pronounced skunklike odor (first brought to my attention by John T. Mickel). This pungent, disagreeable odor is noticeable from more than 10 m in the field and can be an aid in locating plants. The compounds responsible disappear during drying and have not been identified, although some mixture of volatile terpenoids is suspected. The species is of further interest within the genus (and among ferns in general) for its geniculate petioles. The petiole bases deviate nearly horizontally from the deepset, nearly erect rhizomes, then curve upward, but the laminae are again oriented nearly horizontally. The leaves thus have a pronounced sigmoidal curvature at maturity.

For a discussion of the rare, sterile hybrid be-

tween this species and *Phanerophlebia juglandifolia*, see the treatment for that species, above.

Representative specimens. MEXICO. **Chiapas:** SW side of Cerro Mozotal, 11 km NW of junction of road to Motozintla along road to El Porvenir, *Breedlove* 41713 (DS). **Guerrero:** El Asoleadero, 15 km W de Camotla, *Rzedowski* 18531 (ENCB). **Hidalgo:** El Potrero, carretera Metepec-Tenango de Doria, *Gimate* L. 975 (ENCB, F, MEXU, NY). **Oaxaca:** 26–29 km NE of Teotitlán del Camino, vicinity of pass at Pto. Soledad, *Mickel & Hellwig* 4156 (NY). **Veracruz:** La Pandura, camino del Ingenio El Rosario a Xico, mpo. Xico, *Narave* F. 319 (XAL). GUATEMALA. **Chimaltenango:** 8 km S of Acatenango, *Madison* 670 (GH). **El Progreso:** between Finca Piamonte and top of Montaña Piamonte, along Joya Pacayal, *Steyermark* 43709 (F, US). **Quetzaltenango:** slopes of Volcán de Zunil at and above Aguas Amargas, *Standley* 65420 (F). **San Marcos:** slopes of Cerro Tumblador, ca. 15 km W of San Marcos, *Williams, Molina R. & Williams* 23058(US). **Solalá:** Volcán San Pedro, N-facing slopes toward Lago de Atitlán, above village of San Pedro, *Steyermark* 47248 (UC). **Suchitepéquez:** Volcán Santa Clara, between Finca El Naranjo and upper slopes, *Steyermark* 46717 (F, US). EL SALVADOR. **Chalatenango:** Cerro El Pital, *Seiler* 418 (F). COSTA RICA. **Cartago:** road up Volcán Irazu, 0.5 mi. above Sanatorio Duran, ca. 9 mi. above Cartago, *Rosbach* 3079 (GH). **Heredia:** N of Heredia, ca. 1 km beyond Porrosatí, *Lellinger & White* 1679 (F, US). **Puntarenas:** upper Río Burú, *Gómez, Chacón, Chacón & Herrera* 21432 (CR, MO). **San José:** Forêts du Copay, *Tonduz* 11930 (US). PANAMA. **Chiriquí:** Volcán de Chiriquí, 7.3+ mi. from Boquete, *Armond* 534 (CAS, F).

6. *Phanerophlebia nobilis* (Schlechtendal & Chamisso) C. Presl, Tent. Pterid. 85. 1836. *Aspidium nobile* Schltdl. & Cham., Linnaea 5: 610. 1830. *Cyrtomium nobile* (Schltdl. & Cham.) T. Moore, Index Fil. lxxxiii. 1857. TYPE: Mexico. Veracruz: Hacienda de Laguna, Oct. 1828, *Schiede* s.n. (holotype, HAL).

Plants not strongly scented; rhizomes to ca. 15 mm diam., erect or ascending, usually unbranched at maturity; rhizome scales 3.5–7.5 mm long, 2–4 mm wide, ovate to elliptic-lanceolate, denticulate or deciduously ciliate, concolorous, brown; leaves to 1.2 m long; petioles shorter than the laminae; petiolar scales sometimes deciduous, dense and overlapping, much like rhizome scales, the broadest ca. 4 mm wide, grading into reduced, hairlike structures above; pinnae (2–)6–17 pairs, to 17 cm long, lanceolate to linear-lanceolate, usually at least somewhat falcate, the apex attenuate, the base obliquely cuneate, rarely subcordate and with an acroscopic auricle, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free or with 1–3 series of areoles toward the margin (these sometimes distributed irregularly), 1–3-branched; sori in 2–4 series between costa

and margin; indusia 0.6–0.9 mm diam., membranous, flat or concave centrally, not umbonate, shriveled at maturity; spores 41–60 μ m long. Chromosome number: $n = 41$.

Two varieties are separable based on differences in venation. These were accorded specific rank by earlier workers, based on the view that reticulate versus free venation was a character of fundamental importance in the classification of *Phanerophlebia* species. The discovery that there are no other morphological characters that reliably separate these two taxa correlates with results from chloroplast DNA analyses, which also suggest a close affinity between the two (Yatskievych et al., 1988). *Phanerophlebia remotispora* has previously been classified closer to *P. juglandifolia* than to *P. nobilis*, based on the assumption that reticulate venation had arisen only once in the group. Studies contrasting *P. juglandifolia* and *P. remotispora* (Yatskievych, 1990; Yatskievych et al., 1988) showed that these two taxa are consistently and readily separable using morphological, isozymic, and chloroplast genomic characters. It is of interest that data from chloroplast DNA analyses also indicated that reticulate venation has arisen independently twice in the genus (Yatskievych et al., 1988).

The varietal designation is here used for two apparently interfertile morphotypes within a species, lacking sharp biogeographic discontinuities, and which are separated only by a single morphological character whose genetic basis remains unknown. The two varieties of *Phanerophlebia nobilis* are sympatric throughout much of Mexico, except for the absence of variety *remotispora* in the northwestern portion of the species' range, but the two varieties have not often been found growing together (see below).

6a. *Phanerophlebia nobilis* var. *nobilis*

Venation free, or with a few, rare anastomoses.

Illustrations. Kunze (1844: pl. 67, as *Aspidium nobile*), Mickel and Beitel (1988: 517).

Phanerophlebia nobilis var. *nobilis* grows in moist soil, rarely on rock faces (in sinks), with limestone, igneous and volcanic substrate; shady, mesic ravines in oak, pine-oak, pine, or pine-fir forests, rarely in cloud forests, often associated with *Alnus*, or other streamside trees; 1000–2800(–3200) m; Mexico (Chiapas, Chihuahua, Distrito Federal, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sonora, Tamaulipas, Tlaxcala, Veracruz), to be

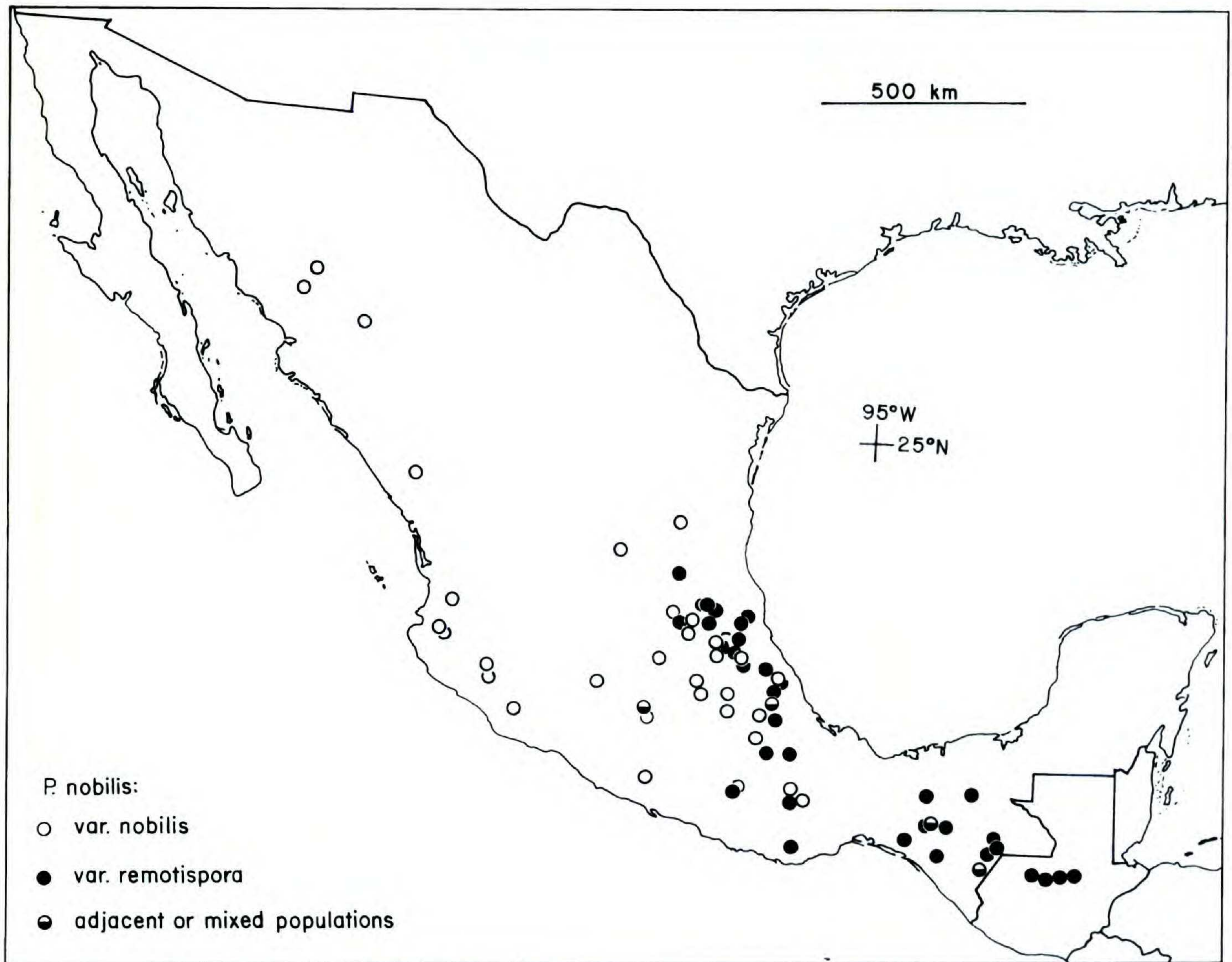


Figure 11. Distributions of *Phanerophlebia nobilis* var. *nobilis* and var. *remotispora*, based upon herbarium specimens examined.

expected in all states except the Yucatán peninsular lowlands and the Baja California Peninsula (Fig. 11).

The single collection known from Chiapas is morphologically atypical and was ascribed to *Phanerophlebia macrosora* by Smith (1981), who also noted its odd morphology. A single specimen labeled as having originated from Brazil (*Rio Grande do Sul*, Porto Alegre, Gebüsch unter der Rua da Independencia, *Reineck s.n.* (GH)) either represents an escape from cultivation or more probably a mislabeled specimen (Alan R. Smith, pers. comm.).

Plants of this variety tend to have somewhat shorter leaves (to 75 cm) than those of variety *remotispora* and commonly have fewer than 10 pairs of lateral pinnae. These differences disappear under common greenhouse culture, and are probably under environmental rather than genetic control. In central and southern Mexico, variety *nobilis* is often found at somewhat higher elevations and in coniferous forests, although there is nearly total congru-

ence of elevational ranges between the two varieties.

Representative specimens. MEXICO. **Chiapas:** Mt. Male, near Porvenir, *Matuda* 4688 (LL, MO, NY). **Chihuahua:** Sierra Charuco, Arroyo Hondo, *Gentry* 7988 (ARIZ, DS, MEXU, MICH, US). **Distrito Federal:** Cañada de Contreras, cerca del Primer Dinamo, *Rzedowski* 27212 (DS, ENCB, F, LL, MICH). **Guerrero:** 32–40 km by road W of Chilpancingo, near and above lumber town of Omiltemi, *Anderson & Laskowski* 4363 (ENCB). **Hidalgo:** 4 km N de Tlahuelompa, mpo. Zacualtipán, *Riba* 66 (MEXU). **Jalisco:** 1 km above settlement of El Isote, in pine-fir zone above Jazmín, NW slopes of Nevado de Colima, *McVaugh* 10125 (MEXU, MICH, MO, US). **México:** 3 km E de San Rafael, mpo. Tlalmanalco, *Cruz C.* 1649 (ENCB). **Michoacán:** Cuincho [Cointzio], près Morelia, *Arsène s.n.* (F, GH, P). **Morelos:** Cerro de El Tepozteco, mpo. Tepoztlán, *Camacho G.* 10–58 (ENCB). **Oaxaca:** trail from San Pedro Nolasco N to the Llano Verde, *Mickel & Hellwig* 3786a (NY). **Puebla:** Puente del Emperador, *Lyonnet* 3240 (MEXU, US). **Querétaro:** Agua Blanca, 10 km S de Pinal de amoles, *Fernández & Zamudio* 992 (MO). **San Luis Potosí:** in montibus San Luis Potosí, *Schaffner s.n.* (NY). **Sinaloa:** 2.8 mi. NE of El Paraiso,

60 mi. SW of El Salto, road between Durango, Dgo. and Villa Union, Sin., *Ownbey & Ownbey 1936* (GH, US). **Sonora:** Curohui, Río Mayo, *Gentry 3660* (ARIZ, GH, MO, UC). **Tamaulipas:** above Casa Piedra on trail to Agua del Indio, region of sierra de Guatemala, ca. 7 km WNW of Gomez Farias, *Johnston 12777* (TEX). **Tlaxcala:** Tlaxcala, près Puebla, *Nicolas s.n.* (A, F, GH, K, MEXU, MICH, MO, P, UC, US). **Veracruz:** head of Orizaba Valley, *Copeland s.n.* (GH, MEXU, MICH, P, UC).

6b. *Phanerophlebia nobilis* var. *remotispora* (E. Fournier) Yatskievych, *Novon* 2: 446. 1992. *Phanerophlebia remotispora* E. Fourn., *Mexic. Pl.* 1: 100. 1872. *Cyrtomium remotisporum* (E. Fourn.) C. V. Morton, *Amer. Fern J.* 47: 54. 1957. TYPE: Mexico. Veracruz: Orizaba, Izhuatlancillo [Ixhuatlancillo], Aug. 1865–1866 [sheet at K = 20 May 1866], *Bourgeau 2349* (holotype, P; isotypes, BM, GH, K, MICH, MO, NY, P, US).

Venation commonly anastomosing toward the margins, with 1–3 series of areoles, these sometimes distributed irregularly. For further comparison with variety *nobilis* see treatment of that variety, above.

Illustrations. Figure 9a'–c'; see also Stolze (1981: 166, as *Cyrtomium remotisporum*), Mickel and Beitel (1988: 520, as *Phanerophlebia remotispora*).

Phanerophlebia nobilis var. *remotispora* grows in moist soil, rarely on rock faces (in sinks), with limestone, igneous and volcanic substrate, in mesic ravines and on slopes, in oak, pine-oak, and pine forests, cloud forests, less commonly in montane rainforests or deciduous or subdeciduous forest associations; also found along brushy roadsides, in overgrown coffee plantations, and in some disturbed or secondary forests; (300–)600–2300 m; southern and eastern Mexico (Chiapas, Hidalgo, México, Michoacán, Oaxaca, Puebla, San Luis Potosí, Veracruz), Guatemala (Fig. 11).

This is the only *Phanerophlebia* taxon to be found in secondary forests or disturbed roadside areas. The single collection from Michoacán is a mixed gathering with the sheet cited from CM representing variety *remotispora* and the other sheets (at A, GH, K, MEXU, MICH, MO, P, and UC) representing variety *nobilis*.

Representative specimens. MEXICO. **Chiapas:** slope of the sumidero in Tenejapa center, mpo. Tenejapa, *Breedlove 10768* (DS, MICH, US). **Hidalgo:** 5 km N de Tenango de Doria, hacia Huehuetla, *Hernández M. 3337* (ENCB, MO). **México:** Los Huevos, Distr. Temascaltepec, *Hinton 403* (NY). **Michoacán:** Cuincho [Cointzio], près Morelia, *Arsène 5415* (CM). **Oaxaca:** vicinity of lumber camp on top of Cerro San Felipe, on road off Axaca–Ixtlán

Highway, 21 km N of Oaxaca, *Hellwig 361* (NY). **Puebla:** Villa Juarez, *Riba s.n.* (MEXU). **San Luis Potosí:** 3 km NE del Ejido de Xilitlilla, mpo. Xilitla, *Rzedowski 10571* (ENCB, NY). **Veracruz:** near Fortín above hydroelectric plant of Cervecería Moctezuma, *Croat 39411* (MO). GUATEMALA. **Alta Verapaz:** along road to El Ester (Lago Izabal), 2 mi. E of Highway 14 to Cobán, *Croat 41442* (CR, MO). **El Quiché:** falls of Río las Violetas, 2.5 mi. N of Nebaj, *Proctor 25446* (LL, US).

The two varieties of *Phanerophlebia nobilis* have only rarely been collected in mixed populations or at adjacent sites. Specimens of intermediate morphology are also occasionally encountered. These are characterized by pinnae with irregularly anastomosing venation, the areolae few and not distributed into a regular, marginal series. Such specimens appear to have well-formed spores. Intermediates between variety *nobilis* and variety *remotispora* include:

MEXICO. **Michoacán:** Cuincho [Cointzio], Río Grande, vic. of Morelia, *Arsène 5961* (GH, MO, US). **Veracruz:** Orizaba, *Fisher s.n.* (MO).

7. *Phanerophlebia pumila* (M. Martens & Galeotti) Fée, *Mém. Foug.* 5: 282. 1852. *Aspidium pumilum* M. Martens & Galeotti, *Nouv. Mém. Acad. Roy. Sci. Bruxelles* 15: 64 + pl. 17, fig. 1. 1842. *Cyrtomium pumilum* (M. Martens & Galeotti) C. V. Morton, *Amer. Fern J.* 47: 54. 1957. TYPE: Mexico. Oaxaca: Llano-Verde et del Carrizal, Mar. 1840, *Galeotti 6251* (holotype, BR, photos, BM, LL, MICH, UC; isotype, P).

Phanerophlebia lindenii E. Fourn., *Mexic. Pl.* 1: 100 + pl. 4. 1872. TYPE: Mexico. Chiapas: in pineto pr. Ciudad Real [San Cristóbal de Las Casas], Mar. [1838], *Linden s.n.* (holotype, P).

Plants not strongly scented; rhizomes to ca. 5 mm diam., usually superficial on substrate, erect or nearly so, not branched at maturity; rhizome scales 3–5 mm long, 2–3 mm wide, ovate to lance-ovate, ciliate-denticulate, concolorous, brown; leaves 4–30(–45) cm long (very short leaves sometimes fertile); petioles shorter than to longer than laminae; petiolar scales usually persistent, densely or loosely overlapping, filiform, the broadest 1.7 mm wide, grading into reduced hairlike structures; pinnae 0–3(–5) pairs, to 8(–12) cm long, ovate to lanceolate, usually somewhat falcate, the apex obtuse to attenuate, the base obliquely subcordate (occasionally cuneate) and sometimes with a small acroscopic auricle, the margins serrulate-denticulate nearly to base, rarely irregularly incised; buds absent from axils of distal pinnae; veins free or uncommonly with few marginal reticulations, 2–3-branched; sori

in 1–2(–3) series between costa and margin; indusia 0.6–0.9 mm diam., membranous, flat or concave centrally, not umbonate, shriveled or subsistent at maturity; spores 41–60 μm long. Chromosome number: $n = 82$.

Illustrations. Figure 12; see also original description, Underwood (1899: pl. 359–360, pinna), Stolze (1981: 166, as *Cyrtomium pumilum*), Mickel and Beitel (1988: 520).

Phanerophlebia pumila is epipetric on sheltered limestone rock faces, particularly those with overhangs, and in sinks; 2100–2950(–3700) m; southern and western Mexico (Chiapas, Guerrero, Michoacán, Oaxaca), Guatemala (Fig. 13).

Phanerophlebia pumila is a morphologically variable tetraploid of presumed allopolyploid origin. Unfortunately, although isozyme studies (Yatskievych, 1990; Yatskievych & Gastony, 1987) have suggested the presence of two parental genomes in this taxon, neither they nor data from chloroplast DNA variation in the genus (Yatskievych et al., 1988) have identified either of the two presumed progenitors involved. On the basis of habitat and morphology, *P. nobilis* may have been involved, but this taxon does not account for the reduced pinna number and leaf size, nor for the characteristic, narrow petiolar scales. One or both diploid progenitors of this species may be extinct, but should be sought by future collectors in the mountains of southern Mexico.

Although *Phanerophlebia pumila* has been characterized by some workers as having extremely reduced leaves with only 1–5 pinnae, the species is, in fact, extremely variable in this regard. Under greenhouse cultivation, plants with only 1–3 pinnae in the field often produced elongate leaves with up to 11 pinnae (also the largest number encountered in the field). Similar observations have been made independently by John T. Mickel (pers. comm.). Different leaves from various individuals of a single Mexican population (Oaxaca, Llano de Las Flores, near km post #130 on hwy. 175, N of Ixtlán de Juárez, Yatskievych et al. 85–139 (CHAPA, IND, MEXU, MO, NY)) display great variation in pinna number, size, shape, and distribution (Fig. 12). Included within the range of variation demonstrated in Figure 12 are leaves referable to *P. lindenii* E. Fourn., a rare morphotype thought to differ from *P. pumila* in its cuneate (rather than subcordate) pinna bases. Larger leaves of *P. pumila* are extremely similar to smaller leaves sometimes displayed by plants of *P. nobilis* growing in ecologically suboptimal sites, such as the edges of sinkholes. Such plants can usually be determined correctly, based

on differences in petiolar scales, but incomplete specimens cannot be determined without examination of stomatal sizes. A single mixed collection of these two species is known (MEXICO. **Michoacán:** Sierra Torrecillas, Distr. Coalcomán, Hinton et al. 12428; *P. pumila* = GH, K, LL, MEXU, MO, NY, US; *P. nobilis* var. *nobilis* = NY).

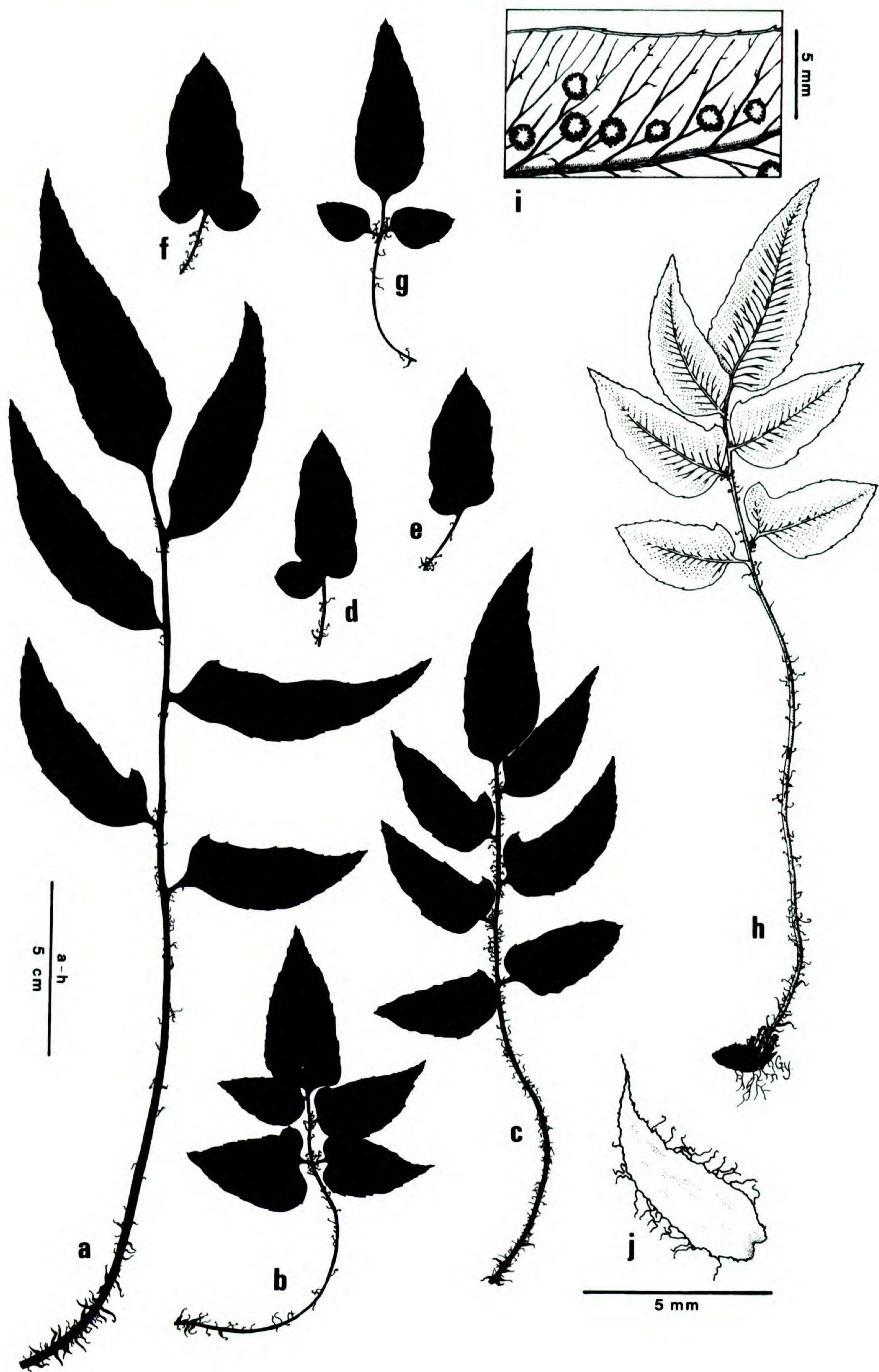
Representative specimens. MEXICO. **Chiapas:** 10 km E of El Porvenir along road from Huixtla to Siltepec, Breedlove & Smith 31816 (DS, MICH, NY, TEX). **Guerrero:** top of the Sierra Madre near Chilpancingo, Nelson 2222 (US). **Michoacán:** Sierra Torrecillas, Distr. Coalcomán, Hinton 15935 (DS, ENCB, F, MEXU, NY, US). **Oaxaca:** trail N of San Pedro Nolasco to the Llano Verde, at the high point above the Llano Verde (Las Cruces), Mickel 5377 (NY). GUATEMALA. **Huehuetenango:** between Tojquiá and Caxín, summit of Sierra los Cuchumatanes, Steyermark 50211 (F, US).

8. *Phanerophlebia umbonata* Underwood, Bull. Torrey Bot. Club 26: 211. 1899. *Cyrtomium umbonatum* (Underw.) C. V. Morton, Amer. Fern J. 47: 54. 1957. TYPE: Mexico. Nuevo León: cool shaded cañons, Sierra Madre, near Monterrey, 14 June 1888, Pringle 1982 (holotype, NY; isotypes, F, GH, MO, NY, P, UC, US).

Plants not strongly scented; rhizomes to ca. 15 mm diam., deeply seated in substrate, short-repent to ascending, often branched at maturity; rhizome scales 2.5–4.5 mm long, 2–4 mm wide, ovate to elliptic-lanceolate, ciliate, concolorous, brown (rarely lighter colored with age); leaves to 90 cm long; petioles shorter than to nearly as long as laminae; petiolar scales sometimes deciduous, dense and overlapping, much like rhizome scales, the broadest ca. 4 mm wide, grading into reduced, hair-like structures above; pinnae 10–18 pairs, to 15 cm long, lanceolate to linear-lanceolate, usually falcate, the apex attenuate, the base cuneate to nearly truncate and lacking an acroscopic auricle, the margins spinulose-serrulate nearly to base; buds absent from axils of distal pinnae; veins free, 1–3-branched; sori in 2–3 series between costa and margin, often submarginal; indusia 0.6–0.9 mm diam., firm, convex with a raised, darker umbo centrally, persistent and not shriveling at maturity; spores 41–60 μm long. Chromosome number: $n = 41$.

Illustrations. See original description; also Knobloch and Correll (1962: 164); Mickel (1979: 164).

Phanerophlebia umbonata grows in moist soil, less commonly among rocks, with igneous and limestone substrate, in sheltered canyons and ra-



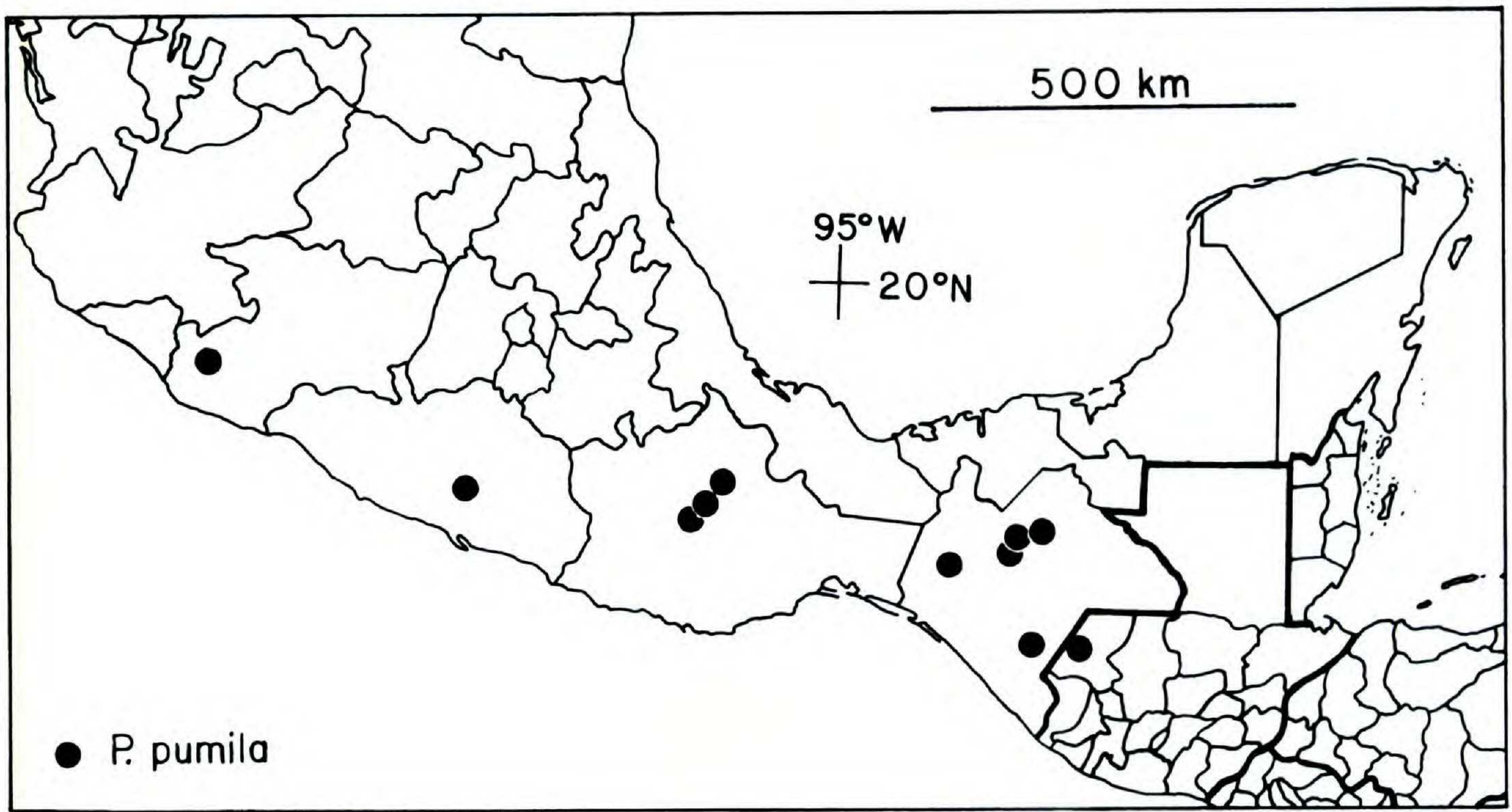


Figure 13. Distribution of *Phanerophlebia pumila*, based upon herbarium specimens examined.

vines, in oak and pine-oak forests, rarely in cloud forests; 550–1900 m; southwestern United States (Texas, known only from the Chisos Mountains in Brewster County), northern Mexico (Chihuahua, Coahuila, Nuevo León, San Luis Potosí, Sonora, Tamaulipas) (Fig. 6).

Phanerophlebia umbonata is easily distinguished from related taxa by its persistent indusium with a raised, central umbo. Incomplete collections of sterile leaves of this species, however, are virtually impossible to distinguish from *P. nobilis* and can be difficult to distinguish from *P. auriculata*. The range of *P. umbonata* is generally to the northeast of that of *P. nobilis* and to the east of that of *P. auriculata*. The latter taxon can also usually be distinguished by its acroscopically auriculate pinnae, which possess a somewhat denser indument of reduced, uniseriate scales abaxially. The diploids *P. nobilis* and *P. umbonata* have been implicated in the parentage of tetraploid *P. auriculata*.

Representative specimens. U.S.A. **Texas:** Brewster County, damp places on side of Casa Grande, basin of the Chisos Mountains, *Warnock 178* (ARIZ, GH, TEX). MEXICO. **Chihuahua:** Guayanopa Canyon, Sierra Madre Mountains, *Jones s.n.* (CAS). **Coahuila:** Cañon de Milagro, E side of Sierra de los Guajes, ca. 12 km W of Hacienda de la Encantada, *Stewart 1532* (GH). **Nuevo León:** steep, rocky slope near Horsetail Falls, 6 km SW of Villa de Santiago, *Clausen 7555* (CU, GH,

MEXU). **San Luis Potosí:** Route 90, 20.0 mi. E of Ciudad de Maiz, *Mickel 563* (ENCB, MICH). **Sonora:** Cañon de Tejas, Sierra Charuco, Sierra Madre Occidental, *Gentry 8119* (MICH, UC). **Tamaulipas:** km 17.6 (11 mi.) SW de Cd. Victoria, carretera 101, *Cowan 3728* (TEX).

EXCLUDED TAXA

- Phanerophlebia aurita* Fée, Crypt. Vasc. Brésil 2: 70 + t. 100, fig. 1. 1873. = *Polystichum auritum* (Fée) Yatskievych.
- Phanerophlebia caryotideia* (Wallich ex Hook. & Grev.) Copel., Gen. Fil. 111. 1947. = *Cyrtomium caryotideum* (Wallich ex Hook. & Grev.) C. Presl.
- Phanerophlebia caryotideia* (Wallich ex Hook. & Grev.) Copel. var. *micropteris* C. Chr. ex Tard., Fl. Madagascar 1: 326. 1958. = *Cyrtomium micropteron* (Kunze) Ching.
- Phanerophlebia falcata* (L. f.) Copel., Gen. Fil. 111. 1947. = *Cyrtomium falcatum* (L. f.) C. Presl.
- Phanerophlebia falcata* (L. f.) Copel. var. *devexicapulae* (Tag.) Ohwi, Fl. Jap. Pterid. 1957. = *Cyrtomium falcatum* (L. f.) C. Presl.
- Phanerophlebia fortunei* (J. Smith) Copel., Gen. Fil. 111. 1947. = *Cyrtomium fortunei* J. Smith.
- Phanerophlebia fortunei* (J. Smith) Copel. var. *cliv-*

←

Figure 12. *Phanerophlebia pumila*. —a–g. Silhouettes of sample leaves from different plants in a single collection. —h. Habit. —i. Detail of pinna. —j. Rhizome scale. (a–j all from Yatskievych et al. 85–139.)

- icola* (Makino) Ohwi, Fl. Jap. Pterid. 69. 1957. = *Cyrtomium fortunei* J. Smith.
- Phanerophlebia fortunei* (J. Smith) Copel. var. *intermedia* (Tag.) Ohwi, Fl. Jap. Pterid. 69. 1957. = *Cyrtomium fortunei* J. Smith.
- Phanerophlebia fraxinella* (H. Christ) Copel., Gen. Fil. 111. 1947. = *Cyrtogonellum fraxinellum* (H. Christ) Ching.
- Phanerophlebia hookeriana* (C. Presl) Copel., Gen. Fil. 111. 1947. = *Cyrtomium hookerianum* (C. Presl) C. Chr.
- Phanerophlebia macrophylla* (Makino) Okuy. ex Ohwi, Fl. Jap. Pterid. 70. 1957. = *Cyrtomium macrophyllum* (Makino) Tag.
- Phanerophlebia macrophylla* (Makino) Okuy. ex Ohwi var. *tukusicola* Okuy., Coll. Ill. Wild Pl. Jap. 7: 41 + pl. 373, fig. 2. 1960. = *Cyrtomium macrophyllum* (Makino) Tag. var. *tukusicola* (Tag.) Tag.
- Phanerophlebia nephrolepioides* (H. Christ) Copel., Gen. Fil. 111. 1947. = *Cyrtomium nephrolepioides* (H. Christ) Copel.
- Phanerophlebia semicordata* (Sw.) Conz., Fl. Taxon. Mex. 1: 13. 1939. = *Cyclopeltis semicordata* (Sw.) J. Smith.
- Phanerophlebia tachiroana* Copel., Gen. Fil., 111. 1947. = *Cyrtomium hookerianum* (C. Presl) C. Chr.
- Phanerophlebia vittata* (H. Christ) Copel., Gen. Fil. 111. 1947. = *Cyrtomium lonchitoides* H. Christ [note that Copeland's use of the name *P. vittata* probably applied to *C. balansae* (Christ) C. Chr., but the type of the basionym *C. vittatum* H. Christ actually = *C. lonchitoides* (Ching, 1936)].
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Appendix I. Exsiccatae.

A. Taxa of *Phanerophlebia* accepted

- (1) *Phanerophlebia auriculata* Underwood
- (2) *P. gastonyi* Yatskievych
- (3) *P. haitiensis* C. Christensen
- (4) *P. juglandifolia* (Humboldt & Bonpland ex Willdenow) J. Smith
- (5) *P. macrosora* (Baker) Underwood
- (6) *P. nobilis* (Schlechtendal & Chamisso) C. Presl
 - (6a) var. *nobilis*
 - (6b) var. *remotispora* (E. Fournier) Yatskievych
- (7) *P. pumila* (M. Martens & Galeotti) Fée
- (8) *P. umbonata* Underwood

B. Collections by collector and number (or collection date where no number was indicated).

Anonymous (det. G. Kunze) (6a); (herb. Jeanpert) without date or number (6b); 000806 (6a); on 26 Apr. 1917 (6b); on 7 Feb. 1919 (1).

Abbon G. [= Arsène 6287] (8); [= Arsène 6291] (8). Acosta & Dorantes 281 (6b). Aguirre C. on 4 Oct. 1975 (8). Alfaro in Feb. 1902 [herb. J. Donnell-Smith 8074] (4); 103 [herb. J. Donnell-Smith 8074] (4). Allart 48 (4). Anderson & Laskowski 4363 (6a). Antonio 1752 (4); 2861 (4). Armond 534 (5). Arreguín 435 (6a). Arsène on 6 July 1911 (6a); on 7 July 1911 (8); 1687 (6a); 5415 (6a, b mixed collection); 5961 (6a, b intermediate). Avendaño R. 00063 (6b).

Ballesteros & Ballesteros 371 (6a), 403 (6a). Barkley 14579A (8). Barkley, Webster (G.) & Rowell 7130 (8). Barrington 1211 (5). Bartlett 10095 (8); 10391 (8); 10406 (8); 10931 (8). Batalla & Bravo on 11 Mar. 1933 (6a). Beaman 3056 (3-vel. aff.). Benson 10947 (1). Berkman & Lee 65 (1). Boege 2737 (6a). Bonilla B. F-4322 (6b). Bonpland without date or locality (4). Botteri 63 (6b). Bourgeau on 20 May 1866 (6b); 45 (6b); 916 (6a); 917 (6a); 104 (6a); 1648 (6b); 2276 (6b); 2341 (6b); 2348 (6b); 2349 (6b). Boutin & Kimnach 3101 (6a). Boza without date or number (4). Brade (A.) 182 (4). Brade (A.) & Brade (C.) on 17 Dec. 1909 [herb. E. Rosenstock 161] (4); 9573 (4). Breckon & Christman 622 (7). Breedlove 7368 (6b); 10768 (6b); 15242 (5); 15299 (5); 24996 (4); 25355 (6b); 25759 (6b); 26262 (5); 26778 (4); 26840 (4); 27697 (6b); 32942 (4); 33657 (6b); 34400 (4); 34615 (6b); 34692 (4); 34698A (4); 38770 (6b); 41708 (4); 41713 (5); 42564 (4);

48670 (4); 53211 (6b). Breedlove & Almeda 56931 (6b). Breedlove & Bartholomew 55521 (7). Breedlove & Dressler 29667 (6b). Breedlove & Smith (Alan) 21652 (2); 21748 (6b); 22330 (6b); 31320 (6b); 31433 (6b); 31495 (2); 31816 (7); 31881 (5); 32310 (6b); 32744 (6b). Breedlove & Strother 46731 (4). Breedlove & Thorne 21363 (6b); 30867 (2). Brenes in 1912 (4). Butterwick 53 (6a). Butterwick & Osborn 2530 (1). Bye 6989 (1); 7094 (6a); 7363 (6a).

Caballero 162 (4). Camacho G. 10–58 (6a). Camp 2561 (1); 2744 (6a). Carrillo 3 (6a). Castillo C. & Vázquez 1360 (6b); 1383 (6b); 1567 (6b). Castillo C., Nee & Benavides 2417 (6b); 2549 (6b). Chacón (I.), Herrera & Gómez (H.) 1765 (4); 1789 (4). Chase 7312 (6a). Chavarría & Lara 27 (4). Cházaro B. & Castillo Ch. 6789 (5). Chrysler 5575 (4). Chrysler & Roeber 5611 (4). Cisneros 1649 (6a). Clausen 7555 (8); 7570 (8). Clewell & Hazlett 3975 (4). Cochrane 8449 (8). Conant 726 (2). Conant, Dorante, Kress & Barrington 727 (6b). Contreras 4956 (6b). Conzatti (C.) 2133 (5). Conzatti (C.), Conzatti (H.) & Gómez (T.) 2363 (5). Conzatti (C.) & Gómez (T.) 3482 (5). Conzatti (C.) & González 1138 (6b). Cooper in 1886(?) (5). Copeland on 13 Jan. 1938 (6a); on 18 Jan. 1938 (6b); on 8 Feb. 1938 (6b); on 21 Mar. 1938 (6b). Cornman 847 (4); 899 (4). Correll 13787 (1); 13788 (1). Correll & Gentry 23043 (1); 23241 (1). Correll & Johnston (I.) 21772 (1). Cory 26488 (8). Cosson 474 (6a). Cota & Gimete 7778 (6b). Cowan 3728 (8). Cowan & Valdés 3586 (8). Croat 39411 (6b); 39484 (6b); 39489 (6b); 39546 (6b); 40940 (4); 41442 (6b); 41474 (6b); 44033 (6b); Croat 46105 (6b); 47628 (4); 48839 (4); 67734 (4). Croat & Hannon 65955 (6b). Cruz C. 1649 (6a).

Darling on 6 Nov. 1961 (1). Darrow & Haskell 2059 (1). Darrow, Gould, Pultz & Phillips (W.) 2556 (1). Davenport without date or number (6a). Davidse 24437 (4). Davis on 7 Apr. 1946 (8). Deaver 4788 (1). del Campo on 11 Mar. 1933 (6a); on 20 May 1933 (6a). Dorfler 190 (4). Dressler 1613 (4); 1947 (8). Drushel 9538 (8); 9539 (8). Dunn (David) & Dunn (Don) 19082 (6b).

Edwards 364 (8). Ehrenberg 868 (6a). Ekman 3119 (3); 7793 (3).

Fendler 233 (4). Ferguson on 23 May 1988 (1). Fernández & Zamudio 992 (6a). Ferris in 1902 (1); 264–08 (1); 294 (1). Fink 62 (6b); Fink 66 (6b). Fisher on 9 Aug. 1924 (6a, b intermediate); on 14 Aug. 1926 (6b); 35365 (6b). Fournier 64 (6b). Fryxell & Anderson 3588 (6b). Funck 211 (4).

Galeotti 6251 (7); 6343 (6a). Gallegos H. 370 (6a). Gentry 3660 (6a); 7988 (6a); 8119 (8). Gereau & Martin 2011 (7). Ghiesbreght without date or number (7); 209 (7); 414 (4). Gilbert 34 (8). Gimete L. 975 (5). Gómez (L.) 360 (5); 528 (4); 3441 (5); 22207 (4). Gómez (L.), Chacón (I.), Chacón (R.) & Herrera 21424 (4); 21432 (5); 21489 (5); 21966 (4). Gómez H. on 3 Oct. 1982 (6a). Gómez-Pompa & Riba 381 (6b). González Q. 1641 (6b); 2419 (6a). Goodding 392–45 (1); 162–50 (1); 138–52 (1); 57–53 (1); 95–61 (1); 3070 (1); 6144 (1); 6145 (1); 6146 (1). Goodding & Hinckley F-3–39 (1); F-9–39 (1). Gould 4347 (1). Gould, Darrow & Haskell 2788 (1). Grant 10799 (4). Grayum, Poveda & Gómez-Laurito 8233 (5). Grayum & Schatz 5166 (4). Guillemín without date or number (6b); in 1866 (6a).

Hahn 172 (6a). Hallberg 848 (7); 1391 (6b); 1456 (6b). Hamilton, Stockwell & Aiello 982 (4). Hammel & Trainer 13825 (4). Hartman 578 (1). Harvey 996 (8). Hellwig 361 (6b); 442.5 (7). Hernández M. 3337 (6b). Hernández M. (R.), Cortés & Hernández M. (I.) 5916 (4). Hernández M.

& Hernández V. 4251 (5). Herrera 3611 (5). Heyde & Lux in Apr. 1892 [herb. J. Donnell-Smith 3259] (6b); 3241 (5). Hinton 403 (6b); 1335 (6a); 3544 (6a); 12428 (6a–7 mixed collection); 15935 (7); 16913 (8); 17511 (8); 17707 (8). House & Andino 961 (4). Hunnewell on 20 Jan. 1941 (5); 14599 (5); 14600 (5).

Jiménez 78–21 (6a). Johnson 699 (6b). Johnston (I.) & Müller (C.) 1362 (8). Johnston (M.) 12777 (6a); 12782 (6a). Johnston (M.), Wendt & Chiang C. 10728 (1). Jones on 23 Sep. 1903 [loc. a] (1); on 23 Sep. 1903 [loc. b] (8). Joyal 1911 (6a).

Karwinski in 1827 (6a). Kearney & Peebles 14485 (1). Kellerman 5774 (5). Kemp in Jan. 1902 (8). Kenoyer in Nov. 1937 (6a); in Dec. 1937 (8); 157 (8); 715 (6a). Kenoyer & Crum 3743 (8). Kerber on 26 Sep. 1882 (6b). Killip 5468 (5); 5488 (4). Knapp 1462 (4). Knobloch 1967 (8); 7011 (1). Koch 7670 (6a). Kruckeberg 4836 (8).

Lacás 154 (8); 247 (8); 371 (8); 486 (8). Lara & Chavarría 28 (4). Laughlin 96 (6b); 549 (6b). Leavenworth 93 (8); 801 (8). Leding 592 (1). Lee, Berkman & Tharp 46193 (1). Leland on 26 Sep. 1896 (8). Lellinger & White 1679 (5). Lemmon in Aug. 1882 (1); on 8 Aug. 1882 (1); on 12 Aug. 1882 (1); in Sep. 1882 (1); 321 (6b). León 17 (4). Leonard & Mickel 4122 (6a). Liebmann in Aug. (6b). Linden in 1838 (7); in Feb.(?) 1838 (7); 1551 (7); 1552 (7). Lint (M.), Lint (H.) & Haskell 1005 (1). Little & Sharp 9922 (7). Loomis & Peebles 5413 (1). Lorence & Cedillo T. 4212 (6a). Lorence, Martin & Cedillo T. 3268 (6a). Lyonnet 87 (6a); 765 (6a); 1481 (6a); 1533 (6a); 1633 (6a); 1926 (6a); 3240 (6a).

Madison 670 (5). Manara on 27 June 1976 (4). Marsh 236 (8); 268 (8); 1871 (8). Martin, Moore & Titley s.n. (6a). Matuda 193 (6b); 1324 (6b); 1365 (6a); 1893 (5); 4068 (5); 4688 (6a); 5230 (5); 18710 (6a); 18783 (6a); 26457 (6a); 28263 (6a); 28304 (6a); 30948 (6a). Maury 6752 (6b). Maxon 4935 (4); 5273 (5). Maxon & Hay 3289 (4). McAlpin 2021 (6b); 2024 (6a). McVaugh 10125 (6a); 11756 (6a); 14238 (6a); 20437 (6a); 22314 (5); 23304 (6a). Mears 231A (6a); 232 (6a). Mexia 1558 (6a). Meyer & Rogers 2581 (8); 2935 (8). Mickel 563 (8); 5377 (7); 6044 (2); 6182 (2); 7248 (6b). Mickel & Hellwig 3786A (5); 3786a (6a); 3786B (2); 4156 (5). Mickel & Leonard 5284 (5); 5384 (7); 5384A (7); 5384B (7). Mickel & Pardue 7047 (6a). Mohr 184 (6b). Montgomery & Root 7339C (8). Moore & Wood 4427 (6a). Morales 1953 (5). Moran 3035 (4); 4167 (4); 5565 (4); 5667 (4); 5706 (3). Morelos O. 5 (6a). Moreno 7014 (4). Moritz 10955 (4). Moya R. 34 (8). Müller (C.) 729 (6b); 2747 (8). Müller (C.) & Müller (M.) 353 (8). Münch in 1901 (6b); in Oct. 1901A (7); in Oct. 1901B (7); 61 (5); 74 (7).

Narave F. 319 (5); 370 (5). Nava & Cruz P. 14 (6a). Nee & Taylor 26813 (6b). Nelson (A.) & Nelson (R.) 1206 (1). Nelson (E.) 2222 (7). Nevling & Gómez-Pompa 2308 (6b). Nicolas on 4 Dec. 1910 (6a). Niles 447 (1).

Ojeda A. 19 (6a). Orzel 79–21 (8). Ownbey (G.) & Ownbey (F.) 1936 (6a).

Palacios-Rios 2901 (2). Palma G. 67 (4). Palmer 450 (1). Parry, Bigelow, Wright (C.) & Schott on 5 Mar. (1). Pennell 16852 (8). Perkins & Hall 3256 (8); 3294 (8). Peterson J-1751 (6a). Phillips (E.) 546 (1); 725 (1). Phillips (W.) & Reynolds 2946 (1). Pineda R. 607 (6a). Pittier 207 (4); 2982 (4). Pringle on 21 July 1884 (1); 3 (1); 831 (1); 1982 (8); 3403 (8); 5585 (6b); 13739 (8). Proctor 25075 (4); 25446 (6b). Puig 4105 (8); 4918 (6b). Purpus in June 1931 (6b); 1595 (6a); 2454 (6a); 2933 (6b); 2993' (6b); 6427 (6b); 15414 (6b); 16024 (6b); 16476 (6b); 16578 (6b).

Rascon without date or number (6b). Rebolledo V. 291 (5). Reeves (B.) et al. 88-1 (1). Reeves (T.) R1202 (1). Reichenbacher 1135 (1). Reichenbacher & Van Devender (T.) 759 (1). Reineck in July 1899 (6a); in Sep. 1899 (6a); on 14 Sep. 1899 (6a). Rhoads in Mar. 1899 (6b). Riba without date or number (6b); 66 (6a); 1002 (6a). Riba, Tryon (R.) & Tryon (A.) 361 (6b). Riskind 1592 (1). Rivera 377 (5). Robinson without date or number (7). Rocha 00071 (8). Rollins & Tryon (R.) 5862 (8). Rossbach 3079 (5). Rowell & Barkley 16M595 (8). Roybal 583 (8); 617 (8). Ruiz O. in Aug. 1947 (6a). Runyon 720 (8); 975 (8); 985 (8). Rzedowski 679 (6b); 10056 (6b); 10571 (6b); 18531 (5); 19864 (6a); 26425 (6a); 27212 (6a); 27229 (6a); 34234 (6a).

Saborio 36 (4). Salinas, Rowell & Barkley 16M575 (8). Salvin 113 (4); without date or number (4, 5 mixed collection). Sánchez (J.) 32 (6a). Sánchez M. 164 (6a). Sánchez S. 445 (6b). Scamman 7087 (5). Schaffner in 1850-1855 (6b); in Aug. 1875 (6a); in 1876 (6a); 67 (6a); 82 (6a); 277 (6a); 461 (6b). Schiede in Oct. 1828 (6a). Seaton 49 (6b). Seibert 187 (4). Seigler (D.), Bohnstedt & Seigler (E.) DS-2550 (8). Seiler 418 (5). Sessé, Mociño & Maldonado 3853 (6a). Shreve 5434 (1). Skutch 742 (5). Smith (Alan) 510 (6a); 515 (6a). Smith (Austin) F24 (4); 48/134 (4); 1463 (4). Smith (C.) on 24 Dec. 1894 (6b); 2187 (6b); 2202 (6b). Smith (R.) M329 (8). Soxman (G.) & Soxman (F.) 362 (1). Spence 27 (6b). Sperling 4958 (2); 4994 (2). Sperry 178 (8). Standley 10468 (4); 32649 (4); 34531 (4 × 5 hybrid); 57840 (5); 60049 (5); 61300 (4); 65420 (5); 67247 (4); 84842 (4); 86672 (4); 87087 (4); 90066 (6b). Stanford, Lauber & Taylor 2085 (8). Stanford, Retherford & Northcraft 1069 (8). Stewart 523 (8); 1532 (8); 1533 (8); 2198 (1). Steyermark 36243 (5); 36871 (4); 37160 (4); 43709 (5); 46717 (5); 47248 (5); 50036 (4); 50211 (7); 55130 (4). Stork 1411 (4); 1558 (4); 1732 (4); 3143 (4). Studhalter 308 (1).

Taylor 364 (8). Tenorio L., Ramamoorthy & Lafrankie 3655 (6b). Tharp on 4 Sep. 1915 (8); 1817 (8). Thornber, Goodding & Nelson (A.) on 16 Mar. 1935 (1). Thorne & Lathrop 41308 (6b); 41784 (6b). Ton 1990 (5); 4840 (6b); 5320 (6b); 5686 (6b); 5889 (6b). Tonduz 11930 (5). Torres

C. (R.), Torres C. (L.) & Martínez 7168 (6b). Torres R. 109 (4). Triana 61 (4). Tucker 1288 (4).

van der Werff & Herrera 7111 (4). Van Devender (T.) on 6 Feb. 1978 (1); on 13 Feb. 1977 (1); on 16 Aug. 1978 (8). Van Devender (T.) & McCarten on 24 Sep. 1977 (1). Van Devender (T.) & Van Devender (M.) on 28 Mar. 1976 (1). Vázquez T. 00345 (6b). Ventura A. 476 (6b); 623 (6b); 2660 (6a); 2694 (6a); 7967 (6b); 9265 (2); 12342 (6b); 13927 (6b); 15836 (6b); 16261 (6b). Verlet in Aug. 1851 (8). Virlet 28 (6a). von Rozynski 415 (8); 646 (8). von Türchheim in Feb. 1856 (6b); in Sep. 1885 [herb. J. Donnell-Smith 768] (6b); in Sep. 1886 [herb. J. Donnell-Smith 1051] (4); in 1907 (6b). Vovides, Rees & Vázquez (T.) 685 (6b).

Warnock 178 (8); 21779 (1). Waterfall 6635 (1). Waters 737 (1). Weber 6046 (5). Webster (G.) & Preston 2878 (8). Webster, (M.) 177 (8). Wendt, Lott & Olmstead 1946 (1). Wercklé 15 (5). White & Chatters 27 (8); 229 (8). Whitehouse on 11 Nov. 1931 (1); on 12 Sep. 1934 (1). Whitchell 16 (8). Whitson 598 (8). Wiggins 7139 (1); 13340 (6b). Williams (L.), Molina R. & Williams (T.) 23058 (5); 23862 (4). Windham 0059B (1); 0109B (1). Wooton on 14 May 1899 (1); on 15 May 1892 (1); on 17 Sep. 1893 (1); on 18 Mar. 1900 (1); on 5 Mar. 1902 (1); 1491 (1). Woronow 3020 (6b). Worthington 7679 (1). Wright (A. H.) & Wright (A. A.) on 8 July 1925 (1). Wynd & Müller (C.) 349 (8).

Yatskievych (G.) 78-361 (1); 83-161 (1). Yatskievych (G.) & Forbes 82-211 (1). Yatskievych (G.) & Gastony 86-250 (8); 86-329 (5); 89-218 (8). Yatskievych (G.) & González L. 85-209 (7). Yatskievych (G.), Hevly & Windham 81-313 (1). Yatskievych (G.) & McCrary 85-05 (8); 86-13 (5); 86-30 (5); 86-31 (4); 86-31a (hybrid of 4 × 5). Yatskievych (G.), McCrary & Worthington 84-67 (1); 84-68(1). Yatskievych (G.), Ranker, González L., Starr (G.) & Starr (C.) 85-139 (7); 85-182 (2); 85-186 (6b); 85-211 (6a). Yatskievych (G.) & Windham 85-296 (1). Yatskievych (G.), Windham & Ranker 83-299 (8); 83-353 (6b); 84-04 (8). Yatskievych (G.), Windham, Ranker & Hallberg 83-467 (5). Yatskievych (G.), Windham & Sullivan 83-10 (1). Yatskievych (G.) & Wollenweber 83-87 (8); 83-128 (6b); 83-158 (6b). Yatskievych (G.) & Yatskievych (U.) 82-273 (1). Young on 4 Sep. 1915 (8).

Zolá B. 00710 (6b); 00742 (6b).